The Fish and Fisheries of Lake Winnipeg: the First 100 years.

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Abstract

This report summarizes information on the fishes and fisheries of Lake Winnipeg. A complete list of species is provided along with their distribution patterns, relative abundances, and predominant habitats. A fundamental component affecting fish distributions is the establishment of fish colonization patterns and historical uses of the fish community. A box model, based on local and literature sources, was constructed to indicate the major components of the aquatic ecosystem leading up to and through Lake Winnipeg's fish community.

Changes in the climate, environment and ecosystem of Lake Winnipeg could alter the fish community. This paper also examines recent range expansions of species in the Red and Assiniboine rivers and in Lake Winnipeg. Using known species preferences and tolerance ranges from literature and local knowledge, probable changes in the fish community in response to potential climate change are postulated. Implications of global warming on the fish community can be surmised using these preference/tolerance ranges.

The history, magnitude and some effects of the commercial, subsistence and recreational fisheries also are documented.

Résumé

Le rapport est un résumé de l'information sur les poissons et la pêche dans le lac Winnipeg. On y trouve une liste complète des espèces, ainsi que de l'information sur leur aire de distribution, leur abondance relative et leurs principaux habitats. Les tendances qui se dessinent dans la colonisation par les poissons et les utilisations historiques de la communauté halieutique sont des facteurs fondamentaux qui influent sur la répartition des poissons. En s'inspirant de sources locales et de la documentation publiée, on a construit un modèle boîte pour indiquer les grandes composantes de l'écosystème aquatique soutenant la communauté halieutique du lac Winnipeg.

Des changements dans le climat, l'environnement et l'écosystème du lac Winnipeg pourraient modifier la communauté halieutique. Le présent article examine aussi l'agrandissement récent de l'aire de distribution d'espèces dans les rivières Rouge et Assiniboine et dans le lac Winnipeg. Les préférences et les limites de tolérance d'espèces recensées dans la documentation publiée et connues localement servent à postuler les changements qui pourraient se produire dans la communauté halieutique en réponse à des changements climatiques potentiels. Il est possible de supposer quelles seront les répercussions du réchauffement de la planète sur la communauté halieutique d'après les préférences et les limites de tolérance des poissons.

L'historique, l'ordre de grandeur et certains effets de la pêche commerciale, de la pêche de subsistance et de la pêche sportive sont aussi documentés.

I. Introduction

Lake Winnipeg, the largest remnant of Glacial Lake Agassiz, is the hub of the Hudson Bay drainage basin. Lake Agassiz, and then Lake Winnipeg have been the distribution centre from which many of the fishes of the drainage basin dispersed. Lake Winnipeg still has the most diverse fish fauna of any water body in the basin. The fishes of Lake Winnipeg are of great economic and ecological significance to the surrounding area. Unfortunately, the composition, abundance, and dynamics of the fish community of Lake Winnipeg are rather poorly understood.

Concerns about the potential downstream effects of invading fish species that might result from interbasin water transfer projects in North Dakota (specifically the Garrison Diversion Project), led the North Dakota State University Water Resources Research Institute to develop an Interbasin Biota Transfer Studies Program which funded a study to examine known biological features of Lake Winnipeg, including the ecology and distributions of the native and exotic fish fauna. Because a comprehensive understanding of the Lake Winnipeg fish fauna was lacking, particularly the nearshore small fish species distributions, the study included a survey of the nearshore fish fauna of Lake Winnipeg and the lower reaches of most of its tributaries. The history of commercial and subsistence fish harvests from the lake was summarized from existing reports in the literature dating back to the late 1870's.

II. Biogeographic History

Glacial Lake Agassiz, in its combined maximal extensions, covered an area of nearly 2 million km^2 (Teller and Clayton 1983) (Figure 1). Prior to deglaciation and the formation of Lake Agassiz, the Laurentide ice sheet covered the area of Lake Winnipeg, so all fish species have entered the area during and after its recession. Events of the Wisconsinan Glaciation and subsequent deglaciation are described briefly in Chapter 1 of this volume and details have been published elsewhere. As the glaciers receded from this portion of the basin, beginning approximately 12,000 years before present (BP) the colonization of fish from several glacial refugia began again.

Crossman and MacAllister (1986) suggested that the present condition of the Manitoba Great Lakes (including Lake Winnipeg) was reached by about 7800 BP. The first access for aquatic organisms to the Lake Winnipeg area (then covered by Glacial Lake Agassiz) probably was northward from the Missourian Refugium, through the area now drained by the South Saskatchewan River about 12,000 years ago. The pathway from the Mississippi River Refugium north via an outlet of Glacial Lake Agassiz, now occupied by the present day Red River, developed simultaneously or shortly thereafter. By 11,000 BP (possibly earlier) connections existed between Lake Agassiz and the Great Lakes. Most species from the Great Lakes also probably originated from the Mississippian Refugium. Crossman and MacAllister (1986) suggested that the Mississippian Refugium (south of the maximum extent of the Wisconsinan ice sheet) was the most important region of dispersal for Lake Agassiz, the Red River drainage, and the Great Lakes, including Lake Winnipeg.

Stewart and Lindsey (1983) suggested that the origins of fish populations might be inferred from present distributions, geographic variation in morphology, habits and ecological tolerances, geological and climatic history of the region and paleontology. Although much of this information is tenuous, they were able to determine the main modes of access by which fish species colonized Lake Winnipeg.

Families, scientific names and common names of the fish species presently known from Lake Winnipeg are given in Table 1. Colonization of the Lake Winnipeg region by fish occurred during three distinct time periods. During the late-glacial period, when Lake Agassiz still was in existence, species entered Lake Agassiz from the Mississippi / Missouri river area, the Great Lakes area and the Bering Refugium (Bering Strait / Alaska area) (Figure 1). All of these species are found well beyond the immediate Lake Winnipeg region, including the Churchill, Red / Assiniboine, Saskatchewan river basins, southern Hudson Bay and James Bay watersheds, the Athabasca and Mackenzie River systems and / or the Great Lakes/St. Lawrence system and beyond. Fish species of this colonization period are all cool / cold water tolerant.

The second colonization period occurred following the drainage of Lake Agassiz. Two routes were possible; an axial dispersal route (Figure 2) via the Minnesota River-Red River mainstem or a northeastern dispersal route (Figure

3) from Mississippi headwaters and/or Lake Superior via the Rainy and Winnipeg rivers.

The fish using these routes fell into three categories. All species in the first group (Table 2A,B) are warm water and turbid water tolerant. All species from the second group (Table 3) are found in the Winnipeg River system, but not in the Red River mainstem or its tributaries in Manitoba except the Assiniboine River. All species in this group are intolerant of turbid water and are warm water tolerant. The third colonizing group (Figure 4) in the post-glacial period arrived by means of both the axial and northeast dispersal routes (Table 4). All these species are found in the Winnipeg River above Great Falls, as well as in the Red and Assiniboine river systems, but do not occur north of the Saskatchewan and Nelson river watersheds, indicating their later arrival in the Lake Winnipeg region. All species in this group are warm water tolerant with a wide range of tolerances of other factors.

Recent additions to Lake Winnipeg's fish fauna include introduced exotic species and new range expansions of species formerly absent from the immediate drainage of Lake Winnipeg but present in headwaters of the Red River drainage in the United States.

There are two ways in which exotic fish reach Manitoba. First and most importantly, there is human introduction, such as authorized and unauthorized stocking of game species, accidental and intentional introductions of live bait or other nongame species (Franzin *et al.* 1994, Carlton and Geller 1993), illegal release of tropical and temperate aquarium specimens (Nelson and Paetz 1992, Hanke and Stewart 1994) and accidental escape from culture ponds (Atton 1959). The second source of exotic biota is by natural dispersal within the drainage from headwaters with intermittent or permanent connection to an adjacent drainage system (Stewart and Lindsey 1970, Stewart *et al.* 1985, McCulloch 1994).

In recent history, several warm water fish species have entered or have been introduced to the Red River and Lake Winnipeg tributaries. Of these recent faunal additions, the bigmouth buffalo, carp, rainbow smelt and white bass have successfully entered Lake Winnipeg (Hanke and Stewart 1994). The stonecat has used Lake Winnipeg to disperse to the Brokenhead River (McCulloch 1994) but has not been collected in the lake itself so far. Similarly, the black crappie has used Lake Winnipeg to disperse into the eastern tributaries but only rarely is collected in the lake.

There are 64 fish species in the immediate basin of Lake Winnipeg and its tributaries (52 in Lake Winnipeg), 58 species in the Red and Assiniboine Rivers and 38 species in Lake Manitoba and its tributaries (Hanke 1996). Presently, there are 16 additional fish species in the Missouri River headwaters that are not known to occur in the Hudson Bay Drainage (Loch *et al.* 1979). Of the 21 species originally described by Loch *et al.* (1979) as being potential invaders of the Hudson Bay Drainage, the smallmouth buffalo (*Ictiobus bubalus*) and yellow bullhead (*Amieurus natalis*) are known from the Red River and/or its headwaters in North Dakota and Minnesota (Koel and Peterka 1994), the rainbow smelt (*Osmerus mordax*) is established in Lake Winnipeg (Campbell *et al.* 1991) and the carp (*Cyprinus carpio*) is widely distributed in the Nelson River Drainage in Manitoba (Atton 1959). The consequences of invasions of new species into the Hudson Bay basin, whether as introduction of exotics by humans or as natural invasions by native species of the Mississippi River basin, are discussed in some detail by Stewart *et al.* (*In Press*).

Remnant (1991) described the original fish community of Lake Winnipeg as having 16 families, 28 genera and 48 species. Presently, due to recent introductions, 52 species of fish are known from the lake and several additional species are occasional occurrences (Table 1). No species have been lost from the community, however the once abundant lake sturgeon population has declined to remnant status and the lake trout continues to be a very rare species in the lake.

III. Field Study

Survey samples were collected at all major tributaries entering Lake Winnipeg upstream to the first impassable waterfall. Samples also were collected from the lakeshore adjacent to tributary mouths (Figure 5). Additional accessible sites on the lakeshore were collected to fill in gaps between rivers. Samples in September of 1989 were collected by the University of Manitoba, Biology of Fishes class field trip along the West side of the lake North to Gull Harbor. Sample sites in the North Basin, (Belanger, Mukutawa, Berens and Poplar rivers in 1991 and Pigeon River in 1992) were accessed by float plane. The Bloodvein River was reached by ferry from Pine Dock, on the West side of the lake. All other sites were accessible by road. Collecting effort was

concentrated in the South Basin of the lake due to better road accessibility.

Collections were made in August of each year except for the Saskatchewan, Dauphin, Jackhead and Fisher rivers which were sampled in the spring of 1992 as weather permitted. Only one sample at the Fisher River was possible due to the weather. Subsequent time constraints and changes to the focus of the project prevented a return trip to the Fisher River in August of 1992. Sample sites were selected to cover all habitat types available.

Specimens in the survey were collected with gill nets, beach seines, electrofishing (Smith-Root Model 12 Electrofisher), set lines, angling, and by dipnet where habitat permitted. The use of several gear types minimized the bias imposed by each individual method (Weaver *et al.* 1993).

Electrofishing was used in fast water in tributary streams and in habitats with obstructions which prevented the use of net gear. Electrofishing consisted of one operator and one or more companion dipnetters. Voltage and pulse frequencies were varied according to the conductivity of the water to maintain a 0.25-ampere peak current through the water sampled. Dip nets were used alone in rock pools with stranded fish or along rock outcrops.

All fish were killed with an overdose of 2-Phenoxy-ethanol before fixation in 10% (vol./vol.) formalin. The abdomens of fish over 15 cm total length were slit open to the right of the midline once dead to allow rapid fixation of the viscera. Fish collected from the survey of 1991 and 1992 were stored in 50% isopropanol (following a one-week rinse in water) while those collected in 1993 and 1994 were permanently stored in the 10% formalin.

Temperature of the lake water was measured with a mercury thermometer at time of sampling. Qualitative descriptions of substrate type, vegetation density, water turbidity, water colour, wood fall, debris or other cover, wave height, water flow, water depth and weather were recorded for each site. A label was added to each collection with location name, time, date and water temperature. At the laboratory, all fish were identified to species and counted except for recently hatched young which were identified to the lowest taxon possible.

Relative abundances of the 43 fish species taken during the distributional survey are shown in Table 5. One percent of the catch approximately equaled 270 individual fish.

Appendix 1 includes the distribution maps of all fish species except those large species that generally are found lake wide and/or are harvested commercially. Other figures with dot maps represent species that have been caught at specific locations and are part of a scientific collection. These species generally are confined to specific habitats or occupy the margins of the basin of Lake Winnipeg.

IV. Distribution of Fishes in Lake Winnipeg:

General presence or absence of species is important in any community study but relative abundance of species is a more useful method of assessing a fish community. Relative abundance can provide a window into the state of the community at a given time period. This window is useful as a point of reference from which to assess future effects of introduced species, environmental changes and anthropogenic practices. Relative abundances of pelagic and inshore fish species in Lake Winnipeg are poorly documented. Generally larger lakewide species are documented and assessed through the commercial fishery.

Table 6 summarizes the origins, general habitat preferences, and relative abundances of Lake Winnipeg fishes. Because fish often move between the lower reaches of tributaries and lacustrine environments, inclusion of a species in one of the habitat categories does not imply complete exclusion from other environments. Species that are abundant and lakewide in distribution but tend to be found mainly in nearshore or offshore zones or in river mouths and associated areas are listed in Table 7 as core fish communities. These are the species one might reasonably expect to find in any sampling of these environments. The distributions of less abundant species in the various environments of the lake can be determined from Table 6.

All but rainbow smelt, cisco, lake whitefish, flathead chub, white bass and spoonhead sculpin also were found frequently in tributaries of Lake Winnipeg. The range of the quillback probably was underestimated by the limited collecting effort in the North Basin. The larger lakewide fishes are known from the commercial fishery and smaller species are collected primarily from nearshore environments. Chestnut lamprey and silver lamprey have been collected only rarely and their distributions are largely unknown.

The distribution of rainbow smelt was inferred from commercial gill net catches in which individual fish snagged their teeth on knots in the meshes. Rainbow smelt also were collected in Playgreen Lake just North of Lake Winnipeg, from stomachs of predatory fish in the forebays of Nelson River impoundments downstream (Remnant *et al.* 1997) and from gillnets in Split

Lake (A. Derksen, MB DNR, personal communication). The flathead chub and spoonhead sculpin were documented poorly by this survey since both species are rare in nearshore environments and rarely or never taken by the commercial fishery offshore. The introduced species that were lakewide include the rainbow smelt and white bass.

Two riverine species, silver chub and river shiner, occur infrequently in Lake Winnipeg but are common in the Red River. Silver chub most often were collected offshore with smaller mesh gill nets. However, one silver chub was collected by seining on the eastern shore of the South Basin of Lake Winnipeg at Hillside Beach.

Riverine species that used Lake Winnipeg for dispersal among tributaries include central mudminnow, bigmouth buffalo, quillback, golden redhorse, white sucker, silver redhorse, shorthead redhorse, carp, golden shiner, weed shiner, mimic shiner, finescale dace, fathead minnow, all catfish, black crappie, rock bass, smallmouth bass, blackside darter and Iowa darter. The lake chub was collected only in the lower Saskatchewan River below the Grand Rapids dam. Of these riverine species, only the carp (Atton 1959) and the smallmouth bass were introduced intentionally to the Lake Winnipeg watershed with subsequent dispersal in Manitoba. Black crappie may have entered Lake Winnipeg via the Winnipeg River and/or from the headwaters of the Red River. Black crappies were collected from the Red River and from tributaries on the east side of Lake Winnipeg north to the Poplar River and on the west side in the Icelandic River. One adult black crappie was noted from the Saskatchewan River (unpublished data) but this survey failed to collect more specimens at this site. The smallmouth bass was collected only in the lowermost reaches of the Winnipeg River just above Traverse Bay. Carp were collected or observed in all Lake Winnipeg tributaries and sporadically collected on lake shorelines. The current northern extreme of the known range of the bigmouth buffalo is the Icelandic River. The golden redhorse was collected in the Red River, a small creek entering the West side of Lake Winnipeg near Ponemah (50° 28' N, 96° 57' W) and the Brokenhead and Winnipeg rivers to the East. Of these riverine species, weed shiner, blackchin shiner, brown bullhead, stonecat, rock bass and blackside darter were not collected from the lake, although they must have used the lake to attain their current distribution.

Species peripheral to Lake Winnipeg and restricted to headwater tributaries include the northern brook lamprey, goldfish, spotfin shiner, hornyhead chub, common shiner, bluntnose minnow, rosyface shiner, sand shiner, creek chub, white crappie and pumpkinseed. The most recent collection of a white crappie in Manitoba was from the Red River at the floodgate south of Winnipeg in September, 1989. A population of goldfish is established in a stormwater retention pond in south Winnipeg and may have entered the Red River via a ditch during spring runoff (Hanke and Stewart 1994). The spotfin shiner apparently has not entered Lake Winnipeg and was collected rarely in the lower Red River. Spotfin shiners were more abundant in the upper Red River and the lower Assiniboine River.

White bass were collected throughout the Red River from Winnipeg to the Red River delta at the South end of Lake Winnipeg. The currently known northern extent of the range of white bass in Manitoba (and in North America) is the mouth of the Mukutawa River (53°10'N, 97° 26'W) on the northeast side of Lake Winnipeg. No white bass were taken from the west side of the North Basin of the lake. White bass were collected throughout the South Basin of the lake.

Sixty seven percent of the fishes of the Lake Winnipeg watershed were headwater and or riverine species that used the lake as a dispersal route or were headwater fish that were not detected in the lake. Many riverine fish were found, but were not common, in nearshore Lake Winnipeg environments.

Our surveys of Lake Winnipeg suggest that invading fishes enter the lake from two southern sources, the Red and Winnipeg rivers. We found no evidence of fish invasion from northern rivers into Lake Winnipeg. Our data do not allow discrimination of entry route for fishes that were found in both the Red and Winnipeg rivers, but the route may be inferred for some species from their distribution patterns in and adjacent to the Lake Winnipeg drainage (Figures 2-4). Recent invaders such as the brown bullhead, golden redhorse and black crappie may have entered the lake from one or both of these rivers. The bigmouth buffalo, golden redhorse and spotfin shiner probably have dispersed naturally from headwaters of the Red River where they have been known since European settlement of these areas. The white crappie probably entered Manitoba by either or both of downstream dispersal following human introduction in the Sheyenne River, a tributary of the upper Red River in North Dakota, or incidentally during introduction of black crappies into Red River tributary waters in Manitoba such as Lake Minnewasta. The recently discovered

presence of the golden redhorse above the hydroelectric dam at Pine Falls (Winnipeg River) suggests that either (1) this species has been in Manitoba longer than previously thought (Franzin *et al.* 1986) (2) has used both recent routes of invasion or (3) was introduced above the Pine Falls dam. The apparent increase in numbers of the golden redhorse and bigmouth buffalo in recent years probably is due to increased collecting effort and/or population increases resulting from the warm period of the late 1980s and early 1990s.

The distribution of fishes in the Lake Winnipeg system fits into four categories, 1) fishes found throughout Lake Winnipeg which we refer to as **lakewide,** 2) species found in the lower Red River and the nearshore areas especially in the South Basin of the lake; referred to as **nearshore**, 3) species found in tributaries that only rarely use the lake; referred to as **riverine** and 4) species that are restricted to headwaters and never enter the lake; referred to as **headwater** (Figure 8). Fishes of the first group are tolerant of turbid lacustrine environments and are found throughout open waters of the lake. Lake whitefish, cisco, goldeye, mooneye, sauger, and walleye are examples of native fishes that are found throughout the lake. Invading species that are tolerant of turbidity, such as the rainbow smelt, white bass, and bigmouth buffalo, potentially may spread from their riverine sources throughout Lake Winnipeg. The two fish in the second group, the silver chub and the river shiner, are common in the Red River but are rare in Lake Winnipeg. The northern extent of the known range of both species is the Narrows of Lake Winnipeg. Fish of the third group, such as black crappie and the golden, weed and mimic shiners, most commonly are collected in clear water but have used the lake to "stream hop" northward to the tributaries up the eastern shore. These fish were able to cross to the west side of the lake at the Narrows and are found in the Icelandic and Fisher rivers. The western side of Lake Winnipeg has only four substantial tributaries (as compared with the eleven tributaries of the east side) and as a result does not appear to be as effective an avenue for dispersal of riverine fish. Blackside darter, hornyhead chub, common shiner and stonecat (McCulloch 1994) are found in the southern-most tributaries entering Lake Winnipeg. These four species are not found in northern tributaries but must have used the lake to attain their present range. Other fish such as the carp, tadpole madtom, channel catfish and bullheads are tolerant of turbidity but more commonly are found in the tributaries of the lake. Their distribution probably reflects selection of low energy environments upstream of river mouths. The faunal composition of the lower reaches of the western tributaries is well known because of intensive collections, with several different gear types, in all rivers except the Mantago and Fisher rivers. Fishes in the fourth group include species such as the lake chub, creek chub, pearl dace, rosyface, sand and spotfin shiners and northern brook lamprey. These riverine fish were not found in Lake Winnipeg, despite extensive sampling around the mouths of the rivers in this survey. Survey collections focused on the lower reaches of the tributaries entering the lake, downstream of the first waterfalls. Few of these waterfalls restrict fish dispersal. The s mpling of headwaters of rivers north of the Icelandic River on the west side and north of the Manigotagan River on the east side, was beyond the capability of this survey. The distributions of headwater fishes in these northern tributaries are poorly known as a result of the limited sampling. Because of extensive sampling independent of this survey, the headwater fish faunas of southern rivers are well known (McCulloch and Franzin 1996, Koel and Peterka 1994, Stewart *et al.* 1985, Scott and Crossman 1979, and unpublished data).

V. Abundance Trends by Latitude:

The ichthyofauna of the South Basin of Lake Winnipeg is homogeneous (Hanke and Stewart 1994), therefore samples from South Basin sites from 1993 and 1994 were pooled for investigation of latitudinal trends. Data for each species were expressed as percent catch for each site. These data from both sides of the lake were grouped to the nearest minute of latitude (Figure 6). Regressions of latitude against abundance were plotted for the commonly caught species (white bass, emerald shiner, yellow perch, goldeye, mooneye, walleye, sauger and spottail shiner) to determine latitudinal trends in abundance. Simpson's diversity index also was used to examine latitudinal trends in species diversity (Figure 7). Simpson's diversity index describes the probability that two specimens randomly drawn from a sample are different species (Krebs 1989).

Knowledge of latitudinal trends in abundance of lacustrine fishes is limited by the limited sampling in the North Basin of the lake. Emerald and spottail shiners and yellow perch appear to be evenly distributed between the two basins of Lake Winnipeg. Since these three small pelagic fish are susceptible to seine collection (Weaver *et al.* 1993) the results are a close approximation of latitudinal trends for these species. White bass in contrast are more abundant in the South Basin and are

rarely collected in the North Basin. In the South Basin of Lake Winnipeg, white bass rival yellow perch as the second most abundant fish in the nearshore environments of Lake Winnipeg. The distribution and abundance described for white bass probably is more accurate than for walleye, sauger, mooneye and goldeye since the young-of-year (YOY) bass remain in shallow water throughout the summer and, like emerald shiners and yellow perch, are susceptible to seine nets. The trend observed in the abundance of the white bass suggests that it is well established in the South Basin and is currently expanding in the North Basin. Most of the white bass collected in the North Basin were YOY and yearlings, indicating that white bass have not reached their physiological northern limit in the lake. The northern limits of warmwater fish species are governed by the length of the growing season and the ability of young to store enough energy to survive their first winter (Shuter and Post 1990).

The latitudinal abundance trends from beach seine samples for walleye, sauger, goldeye and mooneye are identical to that of white bass, but the known distributions of these fish (Heuring 1993, Remnant 1991, Davidoff 1978, Hagen 1978, Kennedy and Sprules 1967) suggest that they are present, but were poorly represented in our limited sampling of the North Basin. In addition, the abundance of walleye, sauger, goldeye and mooneye in northern collections probably is underestimated due to their ability to evade the seine net (Neilsen and Johnson 1989). Gill net samples perhaps would overcome some of the size bias imposed by the seine net (Weaver *et al.* 1993) for these four pelagic species. The presence of the goldeye, mooneye, walleye and sauger in the South Basin shows that they are found in the presence of the white bass. The current survey represents a short time interval and since there are no comparable collections from previous years, no assessment of changes in abundance after the appearance of the introduced white bass is possible.

Invasions of exotic fish into freshwater systems threaten native species and community stability (Prout *et al.* 1990). The success of a species entering a community that presents little or no competition with it for abundant resources is not influenced by that community's pattern of resource use (Sale 1974). The interaction among species therefore would not tend to reduce overlap in abundant or non-limiting resources and overlap would be greater than if competition had influenced the establishment of the community (Sale 1974). Since there is no evidence of either a northward shift in the distribution or shift in habitat use of native fishes in the presence of the invading white bass, the white bass and the native ichthyofauna probably coexist with minimal interaction. Species segregation usually occurs by habitat (Werner *et al.* 1977) with species diversity within a lake being related to habitat heterogeneity (Eadie and Keast 1984). Schoener (1974) also states that resource partitioning usually occurs spatially, with trophic and temporal segregation being more rare. The uniform sandy shorelines of Lake Winnipeg appear to have only 1) pelagic offshore, 2) pelagic inshore and 3) benthic habitats. The benthic substrate grades from sand offshore to coarse gravel inshore. Aquatic macrophyte beds are usually restricted to tributaries because of the turbidity of the lake. The sparse rocky habitat along the west side of the South Basin is almost entirely man-made, consisting of harbors and rock breakwaters. The offshore community was not sampled in this survey of the lake.

VI. A Tentative Ecosystem Model of Lake Winnipeg's Fish Community

Queries of the data in Table 6 were used to partition the fish community of Lake Winnipeg into mainly pelagic and benthic components and into major trophic guilds (planktivores, omnivores, invertivores, piscivores; Table 8). Combining these data into box models provides tentative food webs for the pelagic (Figure 9) and benthic (Figure 10) fish communities indicating the major pathways of energy flow in the two main subsystems in Lake Winnipeg. These models were devised based on literature data from a number of general sources (Scott and Crossman 1979, Becker 1983) and local knowledge. The models are not rigid, quantitative structures but are illustrative of the major components of the food web and obviously overlap in the nearshore area of the lake. Microbial production in both models includes detrital breakdown of dead material from all higher components.

VII. Fisheries of Lake Winnipeg

Biogeographical and ecosystem evidence provides the basis for understanding the origins and composition of the fish community of Lake Winnipeg. Undoubtedly aboriginal peoples used various fish species for thousands of years following human occupation of the Lake Winnipeg region. Fish catches were not documented until Europeans settled the area around the lake; however these historical data provide information

on changes in relative abundance of fish species and community composition as the fishes of Lake Winnipeg were commercially harvested. Management of the commercial fisheries of Lake Winnipeg began as a federal responsibility in the early years but has been under provincial jurisdiction since the transfer of powers in the natural resource sector in 1930. Over the course of the history of the fishery on Lake Winnipeg there have been many variations in the management of fishing effort through regulations of quota and gears; these aspects of the fishery are not within the scope of this paper.

The Commercial Fishery

The commercial fishery began in the 1870's but records documenting catches are available from 1883, with the development of the first viable commercial fishing industry. Heuring (1993) summarized commercial fishing statistics from the 1883 to 1991. Figure 11 shows the distribution through that period of total annual commercial landings of all species of fish from Lake Winnipeg while Figure 12 summarizes 10 year averages of commercial harvests of the three species, lake whitefish, walleye and sauger, which have dominated the commercial harvest over the period of record. Total catch of the main commercial species for the period 1883-1990 are shown in Figure 13. Market demand, market prices, fishing effort and other variables significantly affect commercial harvests. Commercial harvests refer only to the portion of the catch that is sold. All unmarketed species are culled from the commercial catch and will not appear in commercial landing records.

Commercially marketed production of all species of fish for Lake Winnipeg was calculated at 2.19 kg/ha/year from 1883 -1991 (Heuring 1993). Lysack (1986a) calculated the long-term mean commercial yield for the period 1931-1983 at 2.57 kg/ha/y, slightly higher than that for the entire period of record and probably reflecting the fully developed fishery that had evolved by the 1930's. The comparable figure for Lake Erie, a similar-sized lake also with a lengthy record of commercial fish catches, but in a slightly warmer climatic zone, was 9.72 kg/ha/y (Matuzek 1978).

Relative abundance of species is a useful way of examining changes in the species composition of Lake Winnipeg. In the absence of unbiased relative abundance data, Figure 14 summarizes the changes in the relative abundance of species in the landed commercial catch in the 108 years of the commercial fishery from 1883 to 1991.

That a commercial fishery can, and in Lake Winnipeg nearly did, extirpate a desirable fish species is exemplified by an historic overview of the sturgeon catch (Figure 15) beginning in the 1890s and ending by the 1920s. In just two decades the sturgeon population of Lake Winnipeg was nearly eliminated. The presence of remnant spawning stocks in a few rivers continues to contribute a few hundreds to a few tens of kilograms of sturgeon to the annual harvest on the lake to the present day.

Cullage, the practice of deliberately dumping a portion of the catch, has been documented in historical records and fishermen still practice it today. Heuring (1993) attempted to estimate cullage from commercial harvests. In a comparison of commercially marketed catches to experimental catches (from the Manitoba Department of Natural Resources) in 1979-1986, she found that cisco (*Coregonus artedi*), burbot (*Lota lota*) and members of the sucker family (*Catostomus* and *Moxostoma* spp.) were highly under-represented in the marketed catch while freshwater drum (*Aplodinotus grunniens*), bullheads (*Ameiurus* spp.) yellow perch (*Perca flavescens*), and goldeye (*Hiodon alosoides*) were less markedly under-represented. Heuring (1993) estimated total annual cullage for the years of the experimental netting study as follows.

	thousands of kg annually
Coregonus artedi	208 - 1,770
Lota lota	52 - 521
Catostomus and Moxostoma spp.	260 - 625
TOTAL	520 - 2,916

This represents a potential annual mean culled harvest of 1.7 million kg. Actual annual mean marketed harvest over this same period was over 7 million kg, suggesting that cullage could be as high as 25% of the total annual commercial harvest. This would suggest that a total of 139 - 186 million kg of several fish species have been harvested and culled over the history of the fishery. Most of the culled fish are returned to the lake directly rather than disposed of on shore.

Other Fisheries

Subsistence or non-commercial harvest of fish has been, and to a lesser extent still is, conducted on Lake Winnipeg. A major use of subsistence fish catches prior to the widespread use of snowmobiles, was as food for sled dogs. This may have equaled or exceeded the catch used for

human consumption. Heuring (1993) reported recorded subsistence fish harvests for all of Lake Winnipeg in the period 1887-1909, at an average annual harvest of 342,456 kg. No records were available after 1909 but subsistence fish use is known to have declined here and elsewhere, as other foodstuffs became more available. A recent study suggests that subsistence fish consumption in the Lake Winnipeg area is now much lower, perhaps less than one-tenth of the amount used in the early years. Wagner (1986) estimated that members of three communities in 1984 consumed only 7.3-12.9 kg per capita per year for a total of about 13,000 kg/y.

Other fishing activities on Lake Winnipeg and immediate tributary mouths include bait and recreational fishing. Centers of activity for these fisheries are in the lower Red River and associated marsh areas but probably fish stocks from Lake Winnipeg support both Lysack 1986b, 1987).

. The main species sought by bait fishers is emerald shiner, the most abundant species in inshore fish catches in our surveys of Lake Winnipeg nearshore areas. Emerald shiners are thought to use the marsh areas in the delta of the Red River for spawning and nursery habitat and bait fishers intercept adults accessing and leaving spawning grounds (Lysack 1987). Lysack reported that bait fishers in the lower Red River in 1983 harvested in excess of 17,000 kg of emerald shiners; or about 9,000,000 fish.

The abundant walleye, sauger and channel catfish populations throughout the open water season attract recreational fishers to the lower Red and Winnipeg rivers. There also is a large winter ice fishery in the lower Red River, especially between the St. Andrews Lock and Dam and Selkirk. In addition to the above three species, anglers on the lower Red River also catch freshwater drum, goldeye and carp. The lower Red River offers some of the finest trophy channel catfish in North America and the large carp are drawing fishers from as far away as the United Kingdom and continental Europe. In excess of 100,000 kg of all species are taken by anglers expending more than 300,000 hours of effort annually in the lower Red River (Lysack 1986b).

VIII. Potential Effects of Climate Warming

Regier *et al.* (1990) suggested that the potential effects of climate change on fishes in lakes will be of three types: 1) direct effects on ecological pathways from local climate to local stocks or associations of fish species; 2) more general ecosystemic pathway effects involving linkages between climatological, hydrological and biotic systems; and 3) more complex effects of pathways that involve human activities that change with climate and the effects of those cultural changes on ecosystems and the biosphere.

The Lake Winnipeg drainage basin is in an area of North America which is expected, under current climate models, to experience summer surface air temperature increases of more than six and perhaps as much as nine degrees Celsius near southern Lake Winnipeg. Resultant decreases in summer soil moisture of more than 30% and perhaps as much as 50% are expected over much of the drainage basin of the lake, combined with lower snow accumulations in winter (Hengeveld 1990). These two predicted trends will lead to an overall reduction in water supply to Lake Winnipeg which could lead to long term lowering of water levels in the lake and important tributaries.

Surface water temperatures of Lake Winnipeg in summer fairly closely approximate mean air temperature, and wind mixing generally prevents the development of stratification except in unusually calm periods. Temperatures in the South Basin of Lake Winnipeg now reach the low twenties Celsius during normal summers, with the North Basin being a few to several degrees lower due to its more northerly location and larger volume. Temperature increases in the range predicted by models for a doubling of CO_2 (Hengeveld 1990) suggest that water temperatures in the South Basin of Lake Winnipeg could approach 27 - 30C, comparable to that seen in the much shallower and smaller Dauphin Lake during hot weather (Babaluk and Friesen 1990). Similarly, water temperatures in the North Basin of the lake could rise several degrees to the mid twenties Celsius.

The ranges of many species of North American fishes are constrained by annual weather patterns (Shuter and Post 1990). Should predictions of climatic warming prove true, simulations (Magnuson *et al.* 1990, Shuter and Post 1990) suggest that cool and warm water species such as Percids, Centrarchids and Moronids will expand their ranges northward in response to the increase in available thermal habitat. This expansion would be facilitated by the increased length of the growing season, increased growth (Hill and Magnuson 1990) and increased over-winter survival of YOY fish (Johnson and Evans 1990, Shuter and Post 1990). Warmer climate also would facilitate earlier spawning of

fish, thereby increasing the length of the growing season for YOY fish. But reduced spring runoff resulting from less winter snow accumulation may reduce available spawning habitat in influent streams. If a net increase in survival of warm water fishes occurred, the resulting increase in fish density would amplify any ecological interactions between fishes (Hill and Magnuson 1990).

The range of cold water adapted species is expected to retreat northward with increasing lake temperature (Meisner 1990). Some Lake Winnipeg fishes, like lake whitefish and cisco (defined as cool water stenothermic species) (Hokanson 1977), would be expected to experience a reduction in suitable thermal habitat, and a northward retreat in range would be expected in a climate warming event. Other Lake Winnipeg fish falling within Hokanson's (1977) temperate meso- and eurythermal categories would be expected to expand their ranges in the lake and disperse northward should the climate warm. One result of climate warming, if predicted changes do occur, would be loss of lake whitefish and cisco from Lake Winnipeg and one might expect rainbow smelt to be erradicated also. White bass, yellow perch, and members of the pelagic cyprinid community (emerald and spottail shiners) would be expected to become more abundant as cisco and rainbow smelt decline. Total productivity of the lake probably will increase in response to a longer growing season with higher temperatures. Loss of cisco and lake whitefish probably will shunt zooplankton production into smaller-sized zooplanktivorous fishes favoured by walleye and sauger over larger-sized prey. The net effect of environmental and fish community change expected under a climate warming scenario may well be more and larger walleye and sauger with higher yields of these two high value species to commercial fisheries. However the question remains; will water supply to Lake Winnipeg be sufficient to maintain both important spawning streams and suitable water quality conditions in the lake?

Summary

1) The ichthyofauna of Lake Winnipeg shows a North-South gradation of species composition (primarily of benthic and riverine species) between the Red River and the two basins of the lake, though the fauna tends to be homogeneous within each basin (Hanke and Stewart 1994).

2) There are no major barriers to dispersal between the Red River and Lake Winnipeg. The ultimate northern limit to species' distributions therefore, probably involves climatic factors such as the ability of YOY to store reserves to survive the first overwinter period of life (Shuter and Post 1990). Of the species that have entered the lake, white bass and rainbow smelt are the most mobile and are now found in both basins. The lack of northern limit to the distribution of white bass within Lake Winnipeg suggests that the critical thermal threshold for the young of these warm water fish may be further north in the Nelson River. Rainbow smelt originated in the Atlantic Ocean and now have reached Hudson Bay via the Nelson River.

3) There do not appear to be declines in abundance or reduction in ranges of indigenous pelagic species in the presence of white bass. In addition, there does not appear to be any habitat segregation among species in the nearshore environment of Lake Winnipeg in the presence of white bass.

4) The addition of new species to a lake can change the trophic structure of a community. The expansion of white bass, and more recently rainbow smelt, may affect the recruitment of the prey species of existing fish. Reduction of abundant prey species may force the major piscivores, such as walleye and sauger, to switch from perch and emerald shiners to other prey species or more probably to rainbow smelt as has occurred elsewhere when rainbow smelt have become abundant. The changes in the trophic structure that may result from the invasion of rainbow smelt may produce effects throughout the Lake Winnipeg ecosystem.

5) Global climate change undoubtedly will result in complex changes to the environment and biotic communities of Lake Winnipeg, the most important of which will be potential effects on water quantity and quality, for these are fundamental to the whole biotic community.

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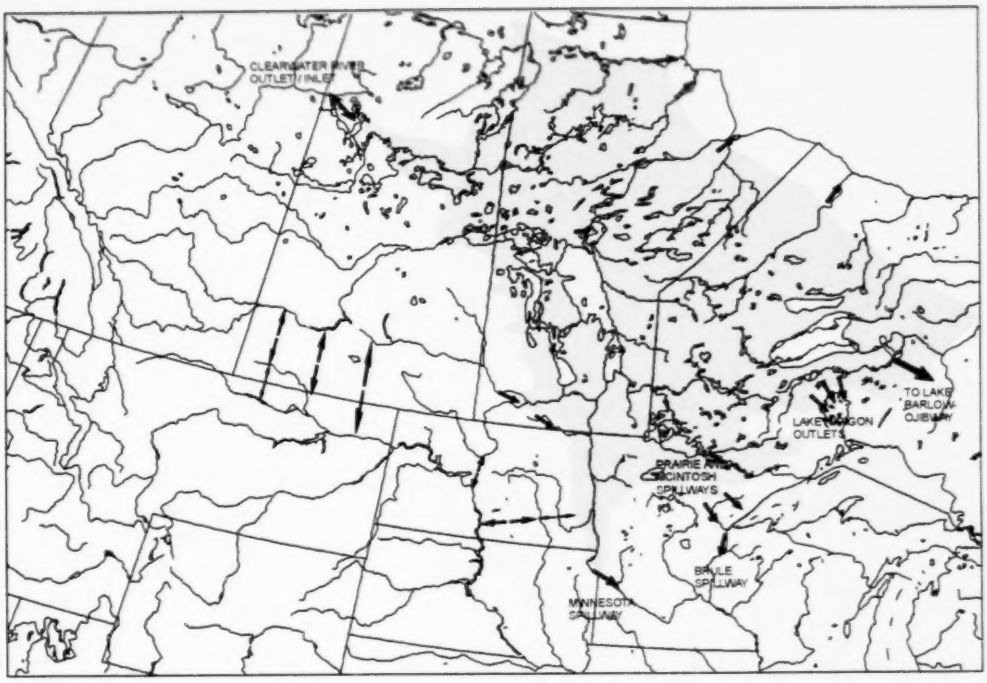


Figure 1. Lake Winnipeg within the context of the composite maximum extent of Glacial Lake Agassiz. At no time did the lake fill the entire shaded area. Known inlets/outlets of Glacial Lake Agassiz are indicated by arrows.(After Teller and Thorleifson, 1983).

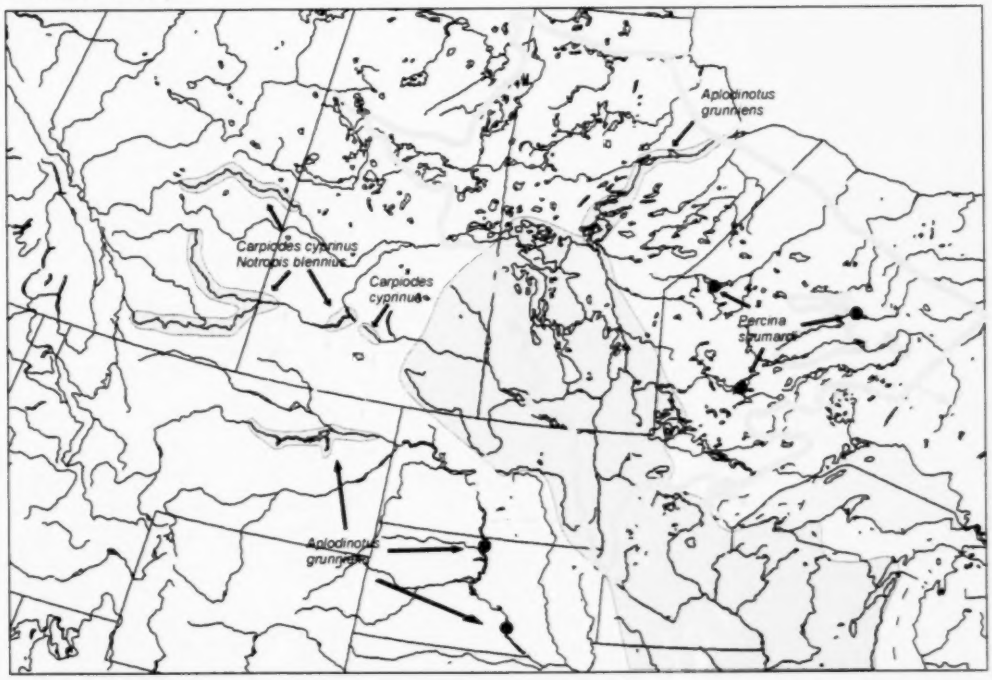


Figure 2. Collective distribution of 32 fish species which entered the Hudson Bay Drainage via a Post-Lake Agassiz -Red River dispersal route (axial dispersal route). See Tables 2A and 2B for species and distribution criteria.

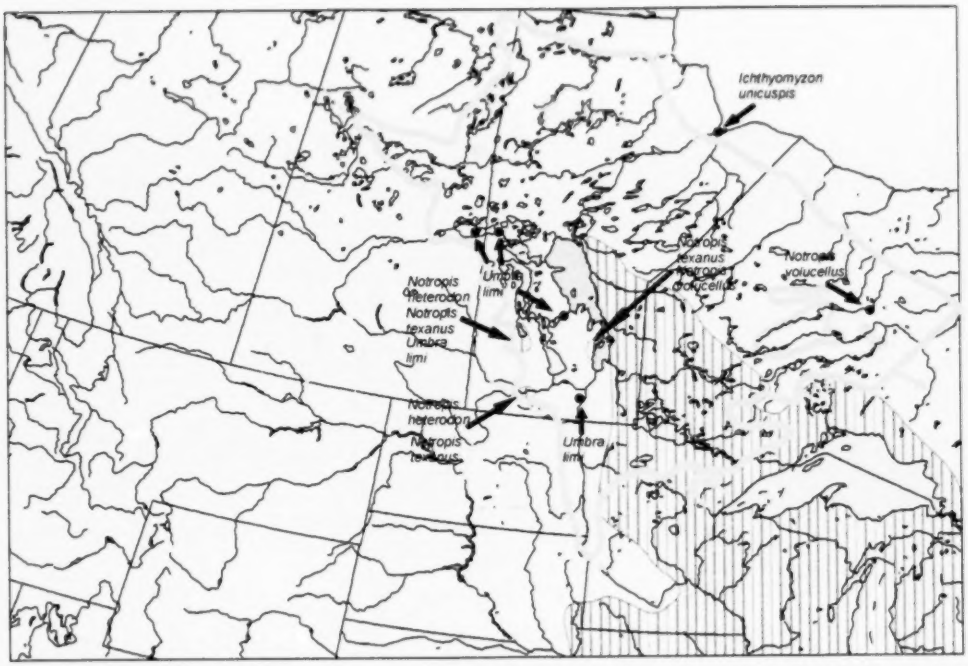


Figure 3. Collective distribution of seven species of fish which entered the Hudson Bay drainage via post -Lake Agassiz Lake Superior / Rainy River dispersal routes. See Table 3 for species and distribution criteria.

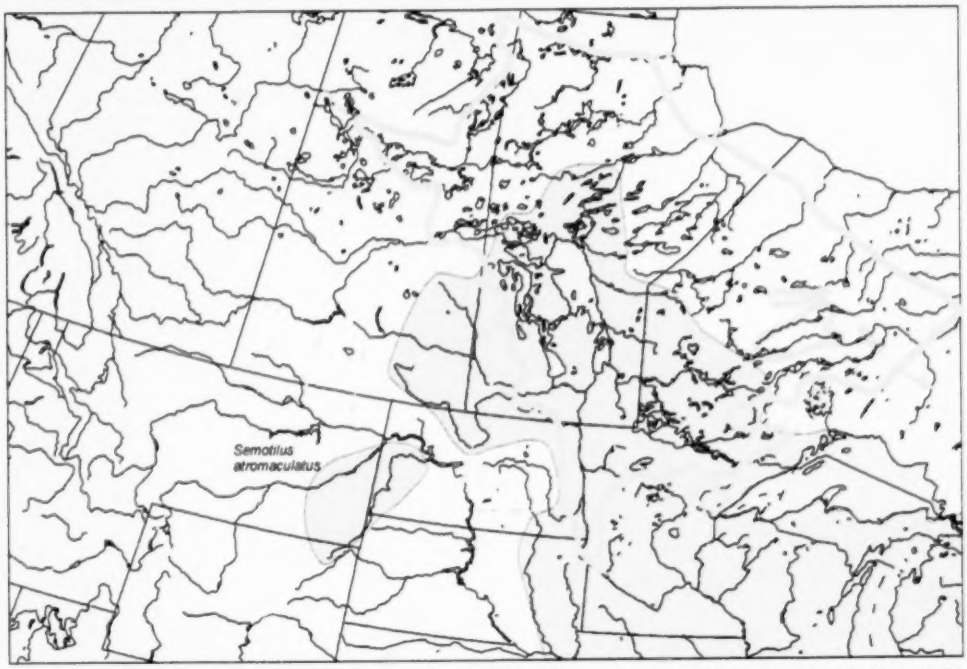


Figure 4. Collective distribution of nine species of fish which may have entered the Hudson Bay drainage via both the Red River and the Lake Superior / Rainy River dispersal routes. See Table 4 for species and criteria.

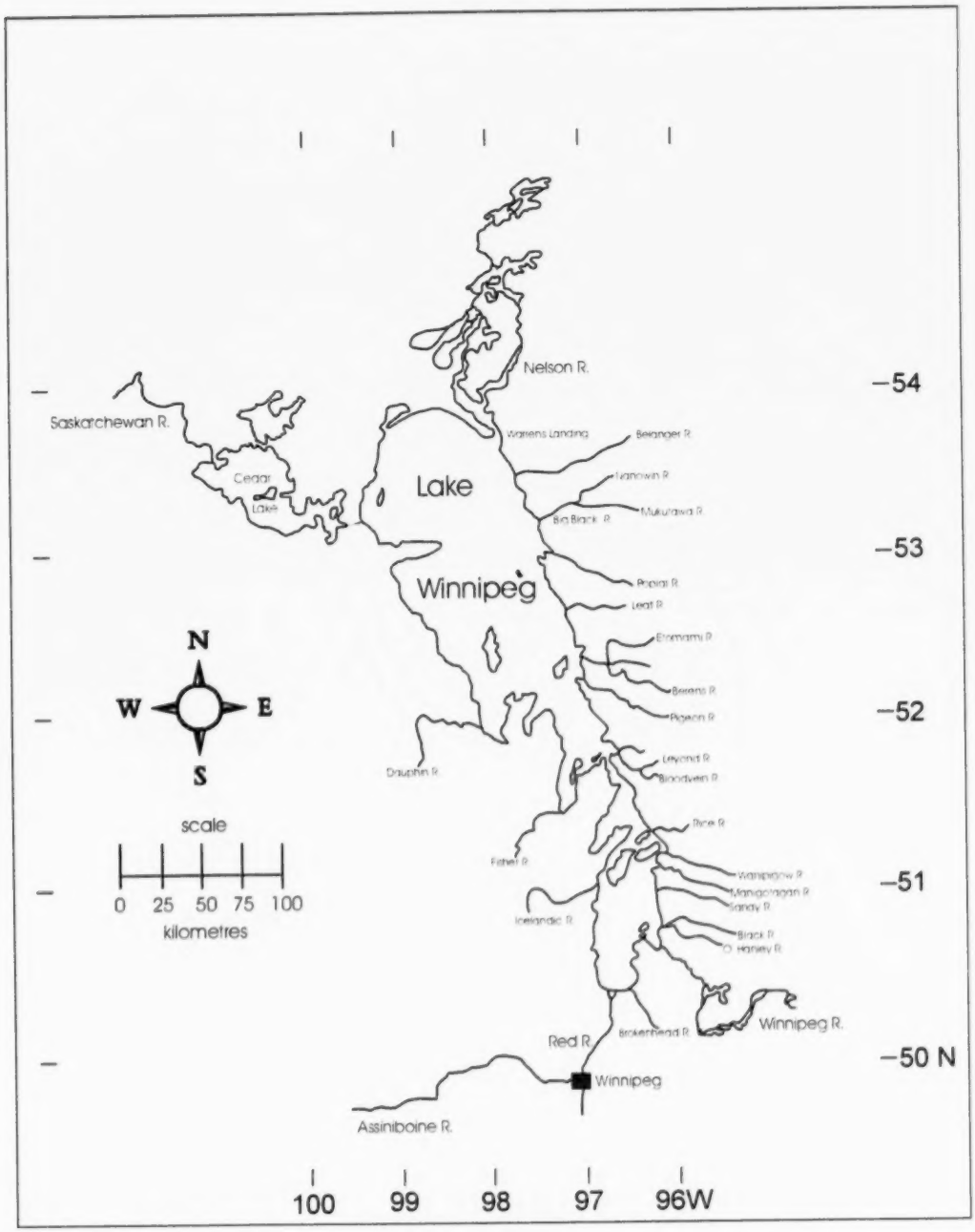


Figure 5. Map of Lake Winnipeg showing river systems sampled between 1991 and 1994.

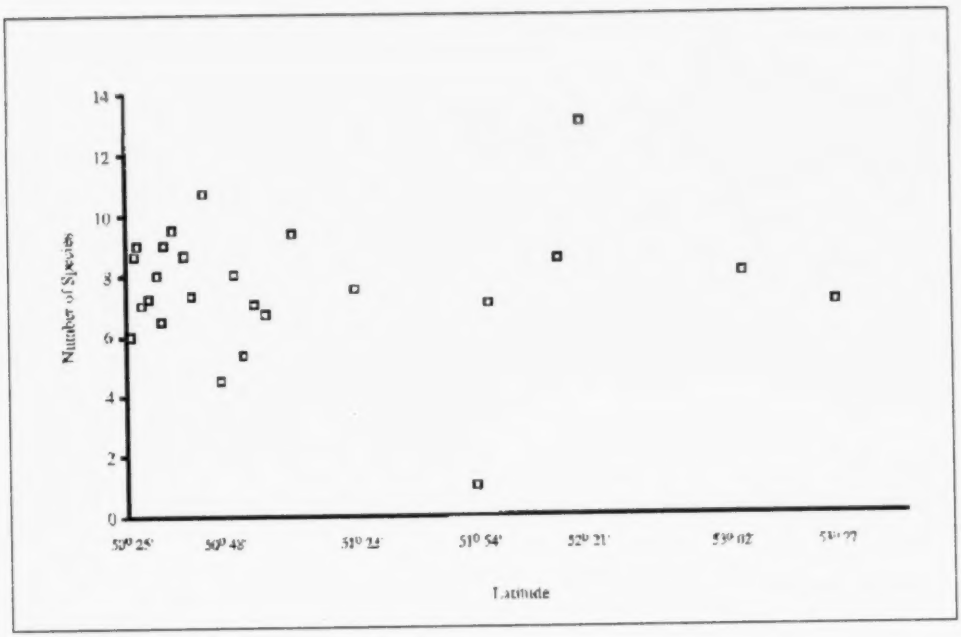


Figure 6. Number of species from seine hauls grouped by the nearest minute of latitude for collections made on Lake Winnipeg shorelines between 1991 and 1994.

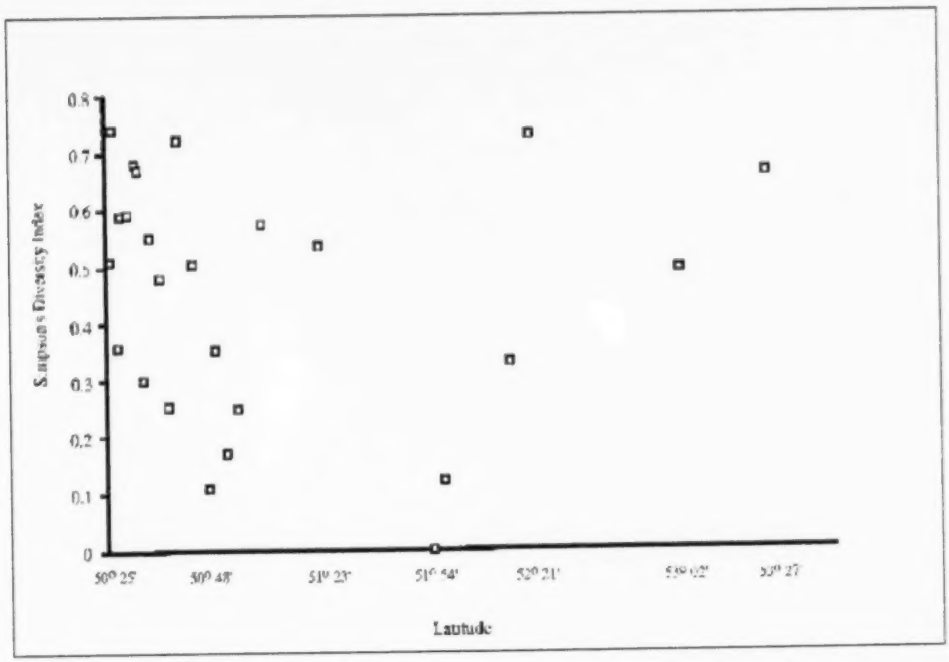


Figure 7. Simpsons's diversity index for seine hauls grouped by the nearest minute of latitude for collections from Lake Winnipeg shorelines between 1991 and 1994.

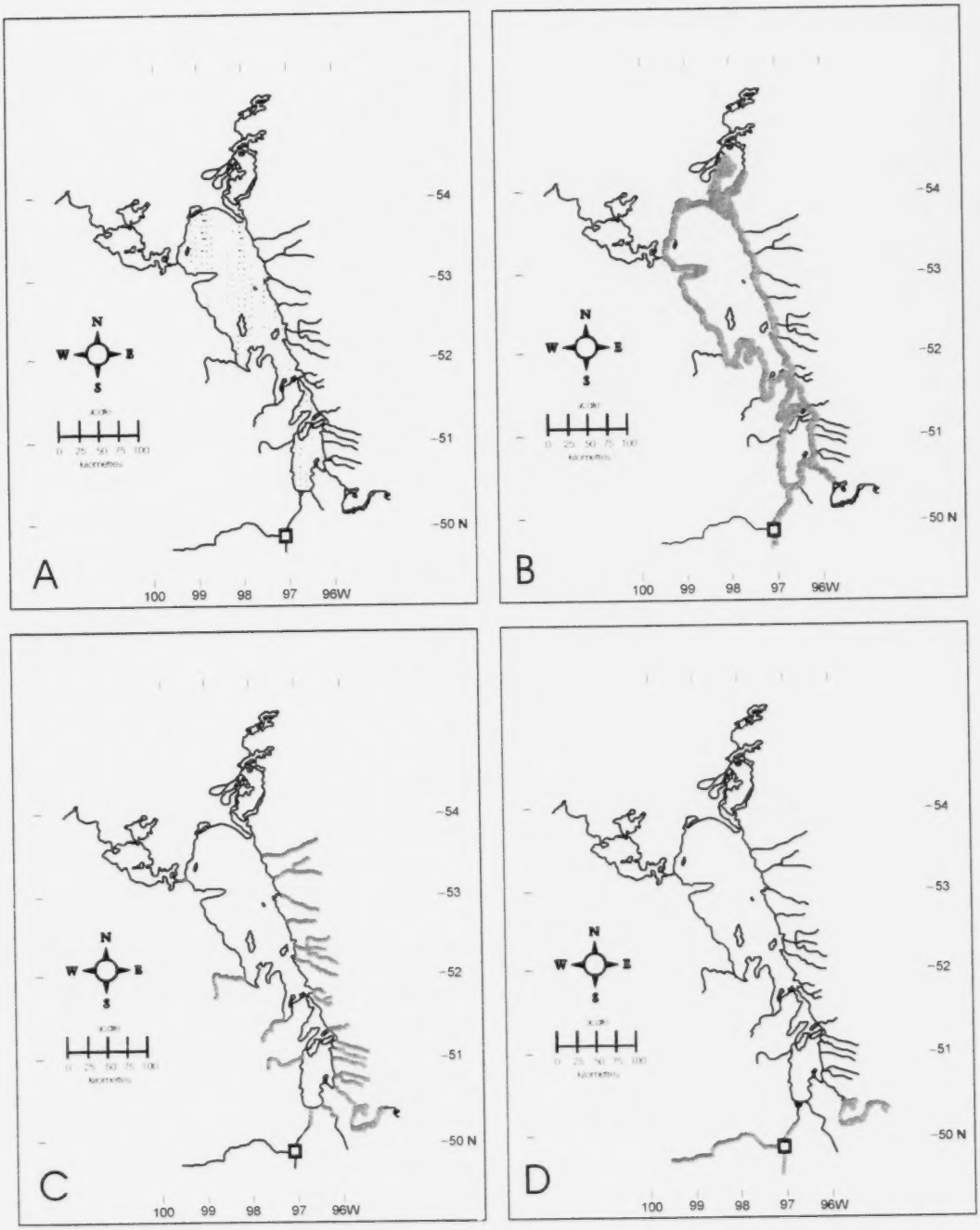


Figure 8. Four maps of general fish distributions in Lake Winnipeg: A) Lakewide; B) Nearshore; C) Riverine; and D) Headwater

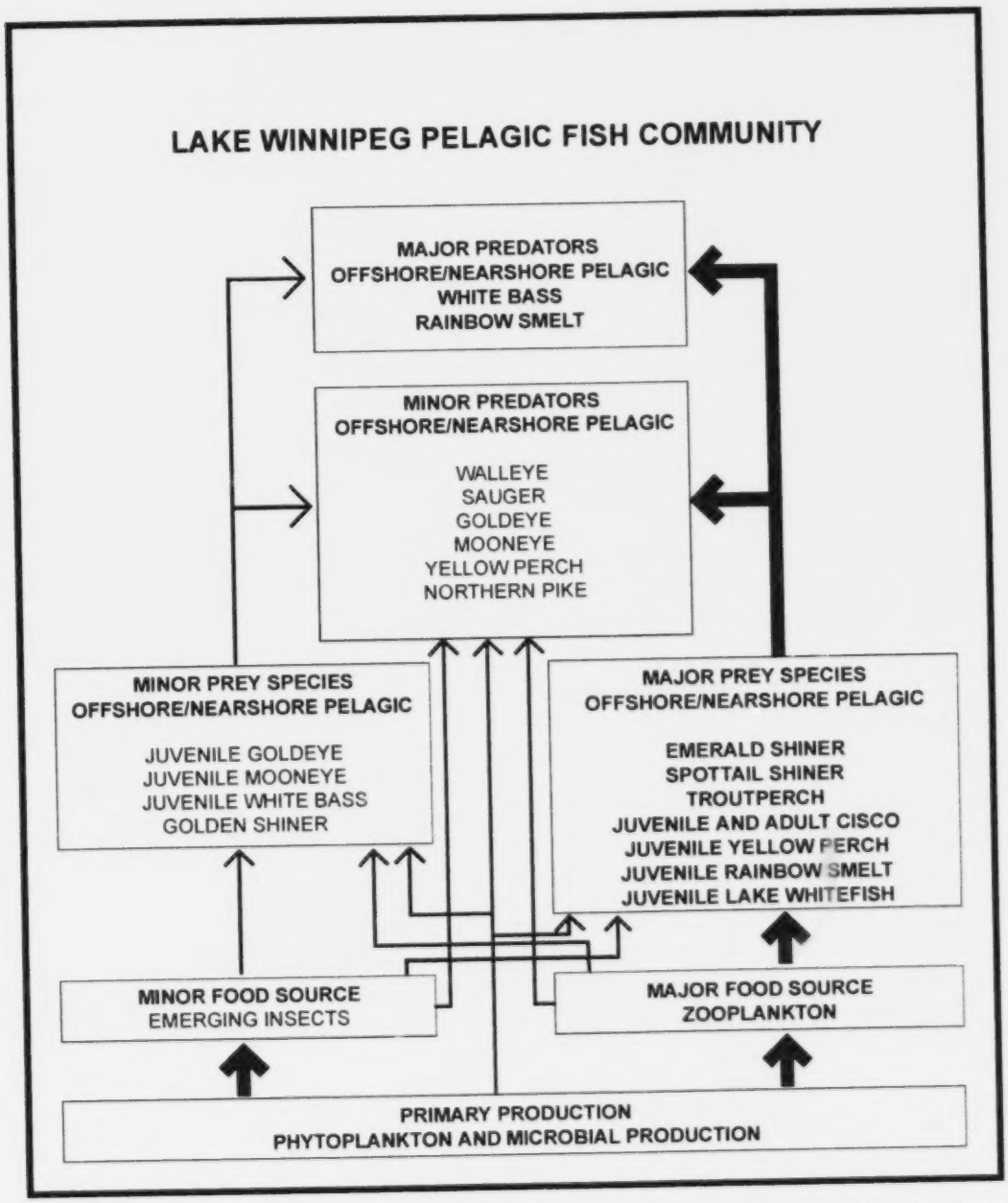


Figure 9. Schematic representation of major food web interactions in the pelagic fish community of Lake Winnipeg.

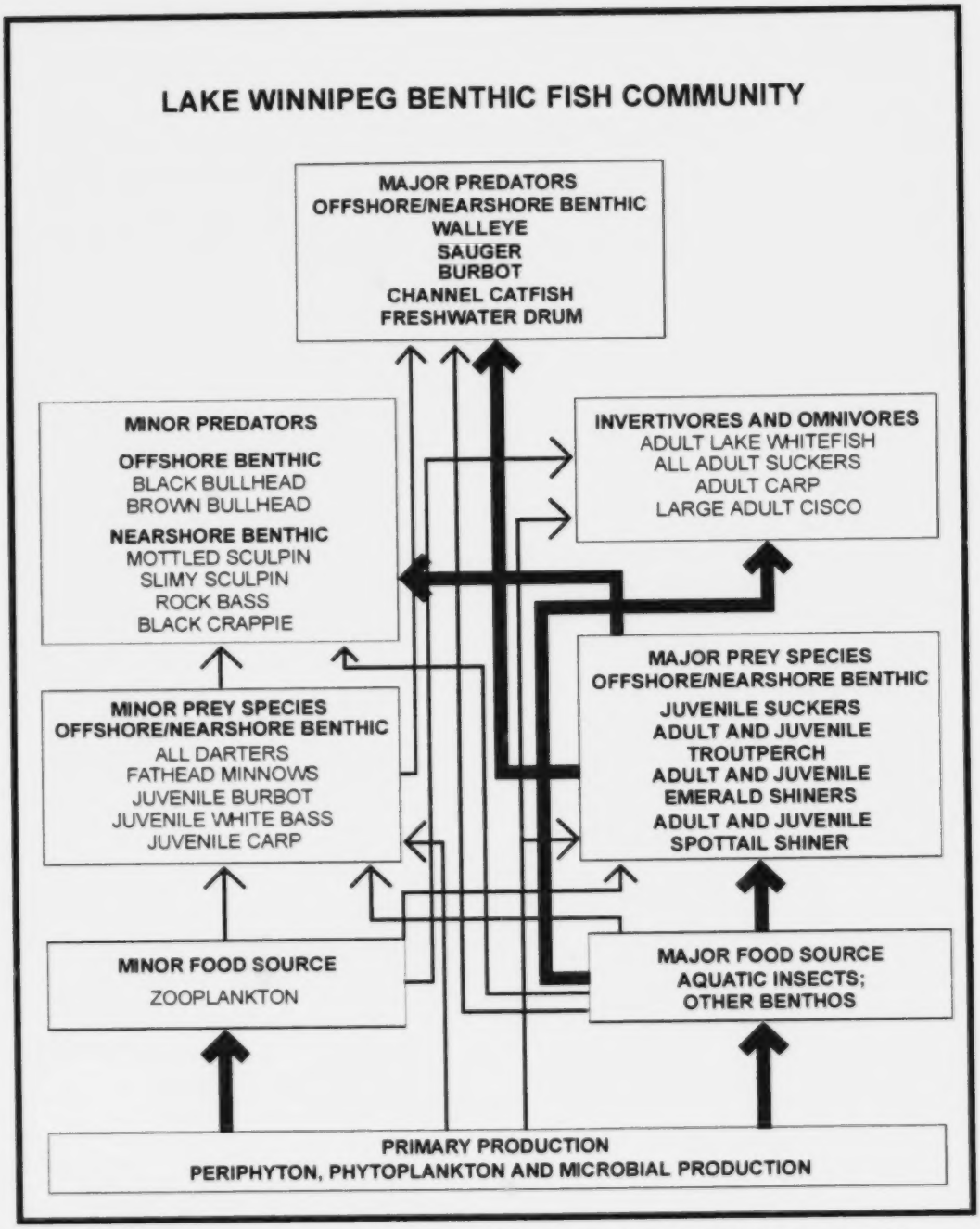


Figure 10. Schematic representation of major food web interactions in the benthic fish community of Lake Winnipeg.

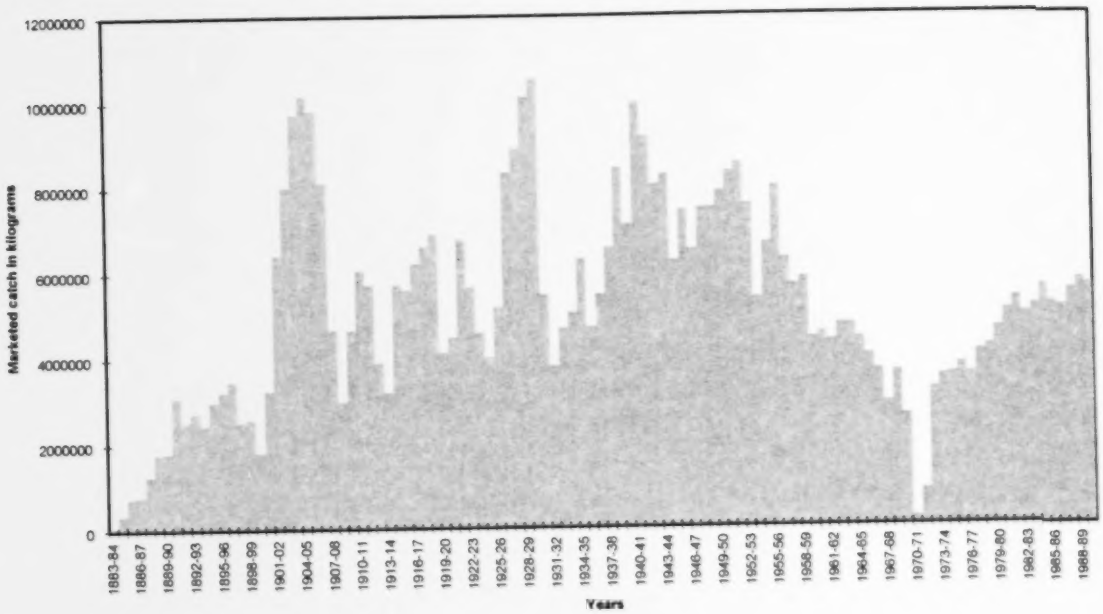


Figure 11. Annual commercial landings of all species of fish from Lake Winnipeg: 1883 - 1990.

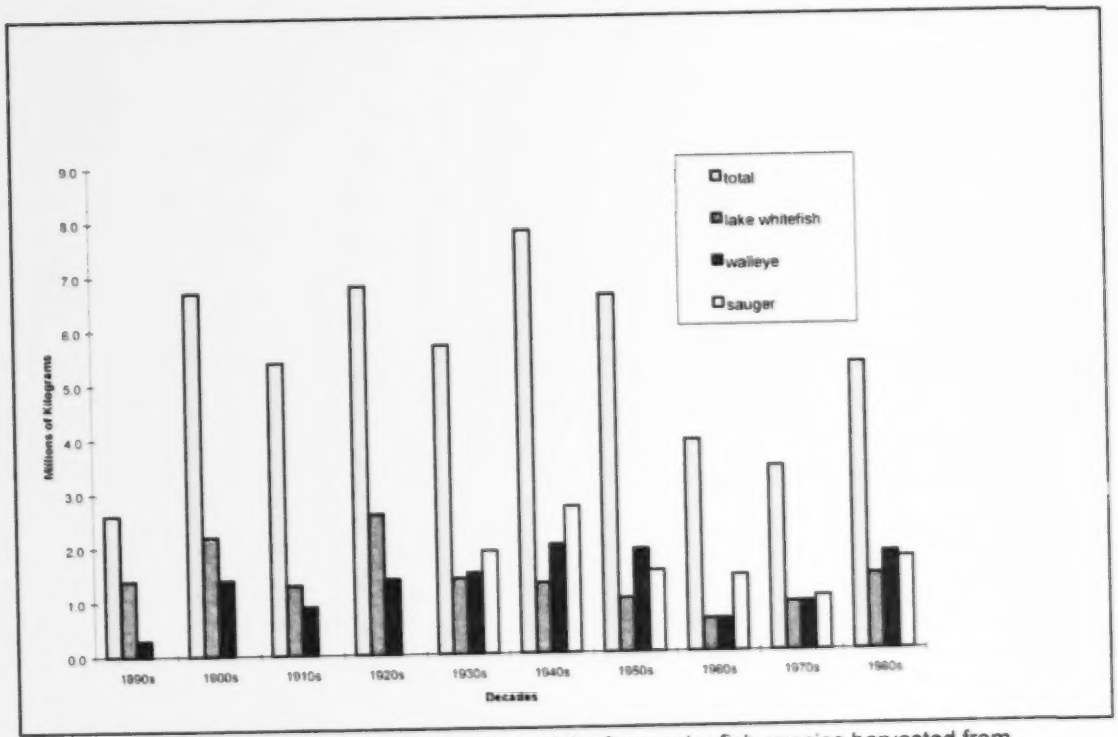


Figure 12. Average annual commercial catches of the four major fish species harvested from Lake Winnipeg by decade from the 1890s to the 1980s.

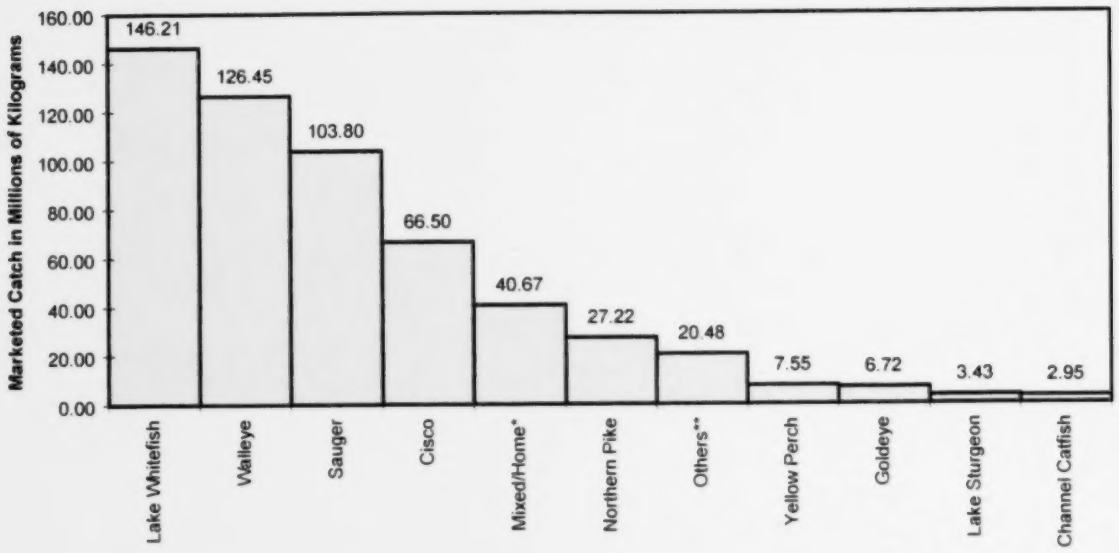


Figure 13. Total commercially-harvested weights of the main fish species in fish catches from Lake Winnipeg: 1880 -1990. See Appendix 2 for detailed catch records.

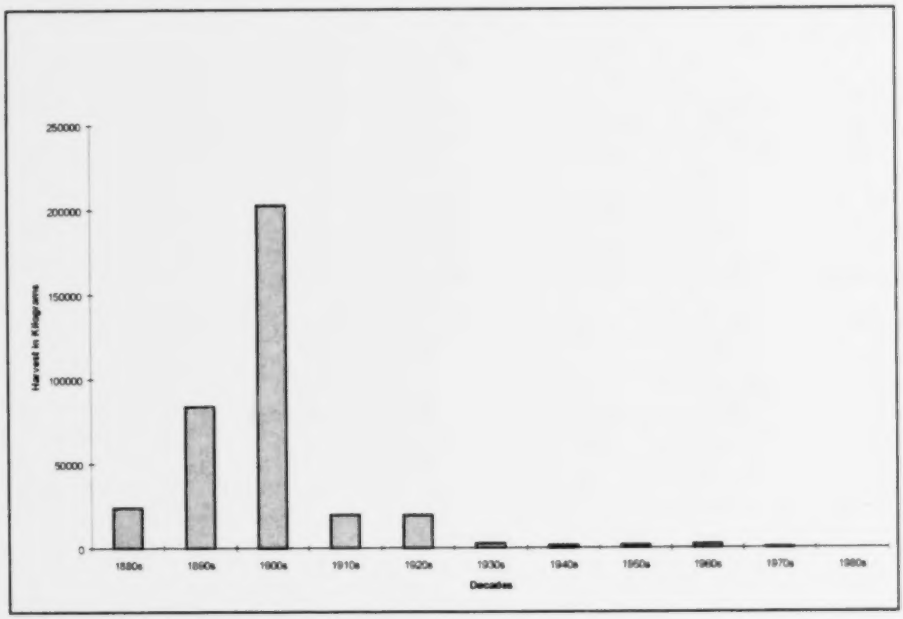


Figure 15. Mean annual catches of sturgeon from Lake Winnipeg by decades from 1883 t 1990. See Appendix 2 for detailed catch records.

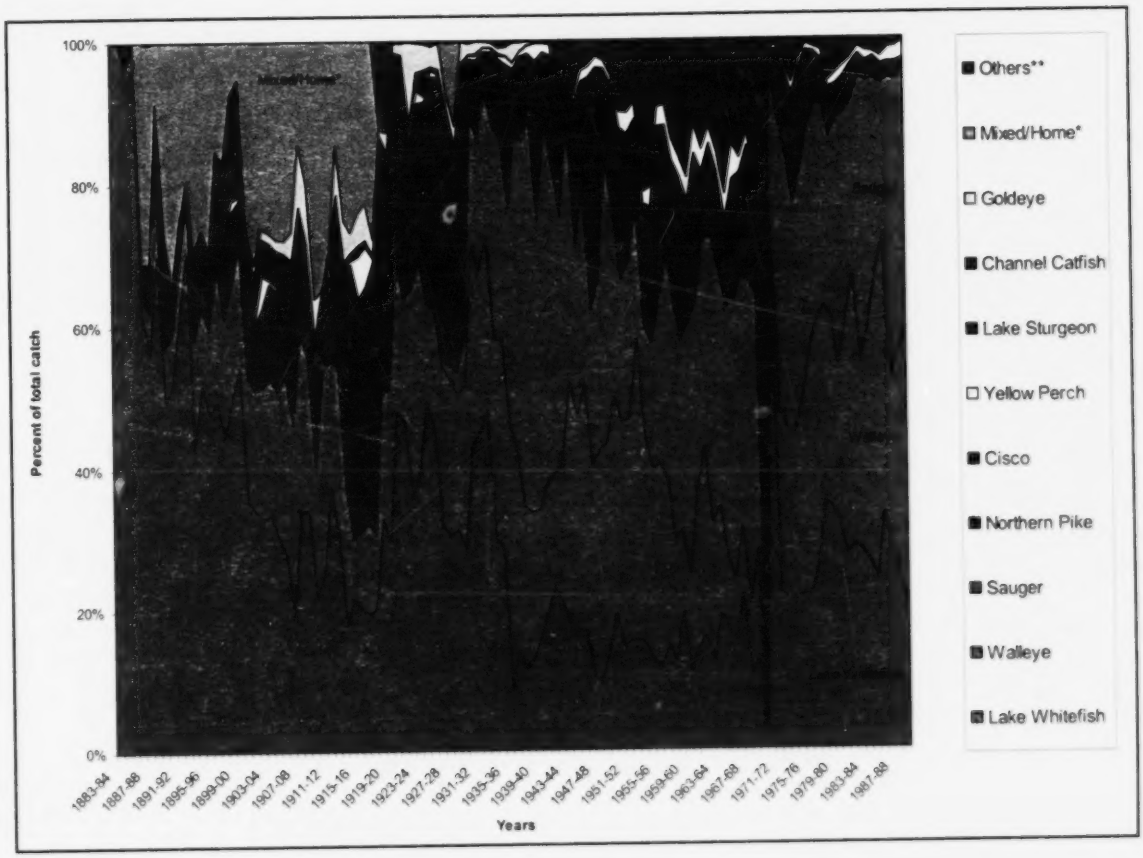


Figure 14. Proportional distribution of the commercially-harvested fish catch from Lake Winnipeg: 1883 - 1990. See Appendix 2 for detailed catch records.

Table 1. Fishes of Lake Winnipeg and its immediate basin.
Highlighted species are unlikely to be found in the lake itself.

Scientific Name	Common Name
Petromyzontidae: Lampreys	
Ichthyomyzon castanaeus	Chestnut Lamprey
Acipenseridae: Sturgeons	
Acipenser fulvescens	Lake Sturgeon
Hiodontidae: Mooneyes	
Hiodon alosoides	Goldeye
Hiodon tergisus	Mooneye
Cyprinidae: Minnows	
Couesius plumbeus	Lake Chub
Cyprinus carpio	Carp
Macrhybopsis storeriana	Silver Chub
Notemigonus crysoleucas	Golden Shiner
Notropis atherinoides	Emerald Shiner
Notropis blennius	River Shiner
Notropis heterodon	Blackchin Shiner
Notropis heterolepis	Blacknose Shiner
Notropis hudsonius	Spottail Shiner
Notropis texanus	Weed Shiner
Notropis volucellus	Mimic Shiner
Pimephales promelas	Fathead Minnow
Platygobio gracilis	Flathead Chub
Rhinichthys obtusus	Western Blacknose Dace
Rhinichthys cataractae	Longnose dace
Catostomidae: Suckers	
Carpiodes cyprinus	Quillback
Catostomus catostomus	Longnose Sucker
Catostomus commersoni	White Sucker
Ictiobus cyprinellus	Largemouth Buffalo
Moxostoma anisurum	Silver Redhorse
Moxostoma erythrurum	Golden Redhorse
Moxostoma macrolepidotum	Shorthead Redhorse
Ictaluridae: Bullhead Catfishes	
Ameiurus melas	Black Bullhead
Ameiurus nebulosus	Brown Bullhead
Ictalurus punctatus	Channel Catfish
Noturus flavus	Stonecat
Noturus gyrinus	Tadpole Madtom
Esocidae: Pikes	
Esox lucius	Northern Pike
Umbridae: Mudminnows	
Umbra limi	Central Mudminnow
Osmeridae: Smelts	
Osmerus mordax	Rainbow Smelt
Salmonidae: Trouts	
Coregonus artedi	Cisco
Coregonus clupeaformis	Lake Whitefish
Coregonus zenithicus	Shortjaw cisco
Salvelinus namaycush	Lake Trout
Percopsidae: Trout-perches	
Percopsis omiscomaycus	Trout-perch
Gadidae: Cods	
Lota lota	Burbot
Gasterosteidae: Sticklebacks	
Culaea inconstans	Brook Stickleback
Pungitius pungitius	Ninespine Stickleback
Cottidae: Sculpins	
Cottus bairdi	Mottled Sculpin
Cottus cognatus	Slimy Sculpin
Cottus ricei	Spoonhead Sculpin
Moronidae: Temperate Basses	
Morone chrysops	White Bass
Centrarchidae: Sunfishes	
Ambloplites rupestris	Rock Bass
Micropterus dolomieui	Smallmouth Bass
Pomoxis nigromaculatus	Black Crappie
Percidae: Perches	
Etheostoma exile	Iowa Darter
Etheostoma nigrum	Johnny Darter
Perca flavescens	Yellow Perch
Percina caprodes	Logperch
Percina maculata	Blackside Darter
Percina shumardi	River Darter
Sander canadensis	Sauger
Sander vitreus	Walleye
Sciaenidae: Drums	
Aplodinotus grunniens	Freshwater Drum

Table 2(A). Fish Species Which Entered the Hudson Bay Drainage Via a Post-Lake Agassiz, Red River Dispersal Route (Axial Dispersal Route, Figure 2).

Species	Common Name
1. *Ichthyomyzon castanaeus*	Chestnut Lamprey
2. *Lepisosteus osseus*	Longnose Gar
3. *Amia calva*	Bowfin
4. *Hiodon tergisus*	Mooneye
5. *Cyprinella spiloptera*	Spotfin Shiner
6. *Macrhybopsis storeriana*	Silver Chub
7. *Nocomis biguttatus*	Hornyhead Chub
8. *Notropis anogenus*	Pugnose Shiner
9. *Notropis blennius*	River Shiner
10. *Notropis dorsalis*	Bigmouth Shiner
11. *Notropis rubellus*	Rosyface Shiner
12. *Pimephales vigilax*	Bullhead Minnow
13. *Carpiodes cyprinus*	Quillback
14. *Moxostoma valenciennesi*	Greater Redhorse
15. *Amieurus nebulosus*	Brown Bullhead
16. *Pomoxis annularis*	White Crappie
17. *Etheostoma microperca*	Least Darter
18. *Percina maculata*	Blackside Darter
19. *Percina shumardi*	River Darter

Criteria

1. These are species with distributions restricted to the southern part of the Hudson Bay Drainage, which do not occur north of the Nelson or Saskatchewan river watersheds.
2. These species occur in the Upper Mississippi River and its tributaries in Minnesota.
3. They also occur in the Red River mainstem and/or tributaries in the United States and/or Canada.
4. They do not occur in the area of the Missouri River Watershed adjacent to the Hudson Bay Drainage, including the James River.
5. They do not occur in the Winnipeg River System upstream of Lake of the Woods.
6. They do not occur in the Lake Superior Watershed north of Lake Superior.

Table 2(B). In addition, the distribution in the Hudson Bay Drainage of the following species supports their also having used the axial dispersal route, even though they violate one or more of the criteria above. They also occur in Lake Superior and/or the Lake Superior Watershed north of Lake Superior.

Species	Common Name	Criteria Violated
1. *Campostoma anomalum*	Central Stoneroller	3 (tribs. U. S. A. only) 3 (James R. SD)
2. *Notropis stramineus*	Sand Shiner	4 (Missouri & James Rs., ND)
3. *Ictiobus bubalus*	Smallmouth Buffalo	4 (Missouri & James Rs., ND)
4. *Ictiobus cyprinellus*	Bigmouth Buffalo	4 (Missouri & James Rs., ND)
5. *Amieurus melas*	Black Bullhead	4 (Missouri & James Rs., ND)
6. *Amieurus natalis*	Yellow Bullhead	4 (Missouri & James Rs., ND)
7. *Ictalurus punctatus*	Channel Catfish	4 (Missouri & James Rs., ND)
8. *Noturus flavus*	Stonecat	3 (Missouri R. ND)
9. *Fundulus diaphanus*	Banded Killifish	4 (James R., ND)
10. *Lepomis cyanellus*	Green Sunfish	3 (tribs. U. S. A. only) 4 (Missouri R. MT)
11. *Lepomis humilis*	Orangespotted Sunfish	3 (tribs. U. S. A. only) 4 (Missouri & James Rs., SD)
12. *Lepomis macrochirus*	Bluegill	3 (tribs only) 4 (Missouri R., MT)
13. *Aplodinotus grunniens*	Freshwater Drum	4 (James R., SD, Missouri R., SD-MT)

Table 3. Fish which entered the Hudson Bay drainage via a post-Lake Agassiz Lake Superior-Rainy River dispersal route. (Northern Dispersal Route, Figure 3).

Species	Common name
1. *Ichthyomyzon fossor*	Northern Brook Lamprey
2. *Ichthyomyzon unicuspis*	Silver Lamprey
3. *Umbra limi*	Central Mudminnow
4. *Notropis heterodon*	Blackchin Shiner
5. *Notropis texanus*	Weed Shiner
6. *Notropis volucellus*	Mimic Shiner
7. *Lepomis megalotis*	Longear Sunfish

Criteria

1. These are species with distributions restricted to the southern part of the Hudson Bay Drainage, which do not occur north of the Nelson or Saskatchewan River watersheds.
2. These species occur in the Upper Mississippi river and its tributaries in Minnesota.
3. They also occur in the Lake Winnipeg and Winnipeg river systems in Manitoba and/or Northwestern Ontario.
4. They also occur in Lake Superior and/or the Lake Superior Watershed north of Lake Superior.
5. They do not occur in the Red River mainstem, but some may be found in Red River tributaries in MN and ND.
6. They do not occur in the area of the Missouri River watershed adjacent to the Hudson Bay Drainage or in the James River.

Table 4. Fish Which Probably Entered the Hudson Bay Drainage Via Both of the Above Dispersal Routes (Figure 4).

Species	Common Name
1. *Luxilus cornutus*	Common Shiner
2. *Rhinichthys atratulus*	Blacknose Dace
3. *Pimephales notatus*	Bluntnose Minnow
4. *Semotilus atromaculatus*	Creek Chub
5. *Moxostoma anisurum*	Silver Redhorse
6. *Moxostoma erythrurum*	Golden Redhorse
7. *Noturus gyrinus*	Tadpole Madtom
8. *Ambloplites rupestris*	Rock Bass
9. *Amieurus melas*	Black Bullhead

Table 5. Abundance of fish species collected in nearshore and river mouth surveys of Lake Winnipeg in 1991 – 1992.

Species	Number	Percent Abundance
Notropis atherinoides	8,910	33.4
Perca flavescens	5,095	19.1
Catostomus catostomus	4,333	16.2
Catostomus commersoni	2,308	8.6
Notropis hudsonius	1,475	5.5
Notropis volucellus	725	2.7
Pungitius pungitius	654	2.4
Pimephales promelas	561	2.1
Notropis chrysoleucas	517	1.9
Notropis texanus	404	1.5
Rhinichthys cataractae	326	1.2
Etheostoma nigrum	252	0.9
Percina schumardi	199	0.7
Notropis heterolepis	130	0.5
Morone chrysops	94	0.4
Sander vitreus	89	0.3
Pomoxis nigromaculatus	69	0.3
Umbra limi	56	0.2
Percopsis omiscomaycus	56	0.2
Ambloplites rupestris	55	0.2
Percina caprodes	46	0.2
Etheostoma exile	45	0.2
Esox lucius	39	0.1
Ictalurus punctatus	38	0.1
Culea inconstans	29	0.1
Noturus gyrinus	27	0.1
Moxostoma macrolepidotum	24	0.1
Cottus bairdi	22	0.1
Couesius plumbeus	22	0.1
Hiodon tergisus	19	0.1
Amieurus melas	19	0.1
Lota lota	16	0.1
Notropis blennius	14	0.1
Amieurus nebulosus	12	<0.1
Moxostoma anisurum	8	<0.1
Aplodinotus grunniens	6	<0.1
Coregonus artedi	5	<0.1
Coregonus clupeaformis	3	<0.1
Carpiodes cyprinus	3	<0.1
Cottus cognatus	2	<0.1
Hiodon alosoides	1	<0.1
Cyprinus carpio	1	<0.1
Total Catch		26,709

Table 6. Origins, habitat preferences and abundances of Lake Winnipeg fish species.

	Colonization Pattern						Habitat												
	Glacial		Post-glacial																
Fish Species	Late-Glacial Mississippi -	Missouri - Great Lakes - Beringian	A) Minnesota/Red River	B) Rainy/Winnipeg River	C) Both A and B	Recent introductions	Cool/cold water tolerant	Warm water tolerant	Turbid cool/cold water tolerant	Turbid warm water tolerant	Pelagic	Benthic	Riverine	Lakewide	Offshore	Nearshore	Adult feeding guild *	ABUNDANCE **	Notes
Petromyzontidae																			
Ichthyomyzon castaneus					•			✓				✓	✓			✓	P	R	Sampling Artifact
Acipenseridae																			
Acipenser fulvescens	•						✓	✓	✓	✓		✓	✓	✓	✓		I	R	Rare, historically moderate
Hiodontidae																			
Hiodon alosoides	•						✓	✓	✓	✓	✓		✓	✓	✓		IP	M	
Hiodon tergisus			•				✓	✓	✓	✓	✓		✓	✓	✓		IP	M	
Cyprinidae																			
Couesius plumbeus	•						✓	✓	✓	✓			✓		✓	✓	I	R	
Cyprinus carpio						•		✓		✓		✓	✓	✓		✓	O	A	Introduced
Macrhybopsis storeriana			•							✓		✓	✓		✓	✓	I	R	
Notemigonus crysoleucas	•						✓	✓	✓	✓	✓		✓		✓	✓	ZO	M	
Notropis atherinoides	•						✓	✓	✓	✓	✓		✓	✓	✓	✓	ZO	A	
Notropis blennius			•				✓	✓	✓	✓	✓		✓	✓			I	M	
Notropis heterodon				•			✓	✓					✓			✓	I	R	
Notropis heterolepis	•						✓	✓					✓			✓	I	R	
Notropis hudsonius	•						✓	✓	✓	✓	✓		✓	✓	✓	✓	I	A	
Notropis texanus				•			✓	✓					✓			✓	I	M	
Notropis volucellus				•			✓	✓					✓			✓	I	M	
Pimephales promelas	•						✓	✓	✓	✓		✓	✓	✓		✓	O	A	
Platygobio gracilis	•						✓	✓	✓	✓		✓	✓	✓	✓		I	R	
Rhinichthys obtusus				•			✓	✓				✓	✓			✓	I	R	
Rhinichthys cataractae	•						✓	✓	✓	✓		✓	✓			✓	I	A	
Catostomidae																			
Carpiodes cyprinus			•							✓		✓	✓	✓		✓	O	M	
Catostomus catostomus	•						✓		✓			✓			✓	✓	IO	A	

Table 6. Continued...

	Colonization Pattern						Habitat											
	Glacial		Post-glacial															
Fish Species	Late-Glacial Mississippi -	Missouri - Great Lakes - Beringian	A) Minnesota/Red River	B) Rainy/Winnipeg River	C) Both A and B	Recent introductions	Cool/cold water tolerant	Warm water tolerant	Turbid cool/cold water tolerant	Turbid warm water tolerant	Pelagic	Benthic	Riverine	Lakeside	Offshore	Nearshore	Adult feeding guild *	ABUNDANCE **	Notes
Catostomus commersoni	•						✓	✓	✓	✓		✓	✓	✓	✓	✓	O	A	
Ictiobus cyprinellus			•					✓		✓			✓			✓	ZO	R	
Moxostoma anisurum					•			✓		✓		✓	✓	✓		✓	IO	M	
Moxostoma erythrurum					•			✓		✓		✓	✓			✓	IO	R	
Moxostoma macrolepidotum	•						✓	✓		✓		✓	✓	✓		✓	IO	A	
Ictaluridae																			
Ameiurus melas					•			✓		✓		✓	✓			✓	IP	M	
Ameiurus nebulosus			•				✓	✓	✓	✓		✓	✓			✓	IO	M	
Ictalurus punctatus			•							✓		✓	✓			✓	P	M	
Noturus gyrinus			•					✓		✓		✓	✓			✓	I	R	
Esocidae																			
Esox lucius	•						✓	✓	✓				✓	✓		✓	P	M	
Umbridae																			
Umbra limi				•				✓		✓		✓	✓			✓	I	R	
Osmeridae																			
Osmerus mordax						•	✓		✓		✓			✓	✓		IP	R / M	Introduced, since 1990
Salmonidae																			
Coregonus artedi	•						✓	✓	✓	✓	✓		✓	✓			ZI	A	
Coregonus clupeaformis	•						✓		✓		✓	✓	✓	✓	✓		I	A	
Coregonus zenithicus	•						✓		✓			✓		✓	✓		I	R	
Salvelinus namaycush	•						✓				✓				✓		P	R	rare, commercial fishery
Percopsidae																			
Percopsis omiscomaycus	•						✓	✓	✓	✓			✓	✓		✓	I	A	
Gadidae																			
Lota lota	•						✓	✓	✓	✓		✓	✓	✓	✓	✓	PI	A	

Table 6. Continued...

	Colonization Pattern						Habitat												
	Glacial		Post-glacial																
Fish Species	Late-Glacial Mississippi -	Missouri - Great Lakes - Beringian	A) Minnesota/Red River	B) Rainy/Winnipeg River	C) Both A and B	Recent Introductions	Cool/cold water tolerant	Warm water tolerant	Turbid cool/cold water tolerant	Turbid warm water tolerant	Pelagic	Benthic	Riverine	Lakewide	Offshore	Nearshore	Adult feeding guild *	ABUNDANCE **	Notes
Gasterosteidae																			
Culaea inconstans	•						✓	✓	✓	✓		✓	✓	✓		✓	I	A	
Pungitius pungitius	•						✓				✓			✓	✓	✓	I	M	
Cottidae																			
Cottus bairdi	•						✓	✓	✓	✓		✓	✓	✓		✓	I	A	
Cottus cognatus	•						✓	✓	✓	✓		✓	✓	✓		✓	I	A	
Cottus ricei	•						✓		✓			✓		✓		✓	I	R	
Moronidae																			
Morone chrysops						•		✓		✓	✓		✓	✓	✓	✓	IP	A	Introduced, since 1962
Centrarchidae																			
Ambloplites rupestris					•			✓		✓			✓	✓		✓	IP	A	
Micropterus dolomieui						•		✓					✓			✓	P	R	Introduced?
Pomoxis nigromaculatus					•			✓		✓			✓			✓	IP	M	Introduced?
Percidae																			
Etheostoma exile	•						✓	✓				✓	✓	✓		✓	I	M	
Etheostoma nigrum	•						✓	✓	✓	✓		✓	✓	✓		✓	I	A	
Perca flavescens	•						✓	✓	✓	✓	✓		✓	✓	✓	✓	IP	A	
Percina caprodes	•							✓		✓		✓	✓	✓		✓	I	M	
Percina maculata			•					✓		✓		✓	✓			✓	I	M	
Percina shumardi			•					✓		✓		✓	✓	✓		✓	I	A	
Sander canadensis	•						✓	✓	✓	✓		✓	✓	✓	✓	✓	P	A	
Sander vitreus	•						✓	✓	✓	✓		✓	✓	✓	✓	✓	P	A	
Sciaenidae																			
Aplodinotus grunniens			•				✓	✓	✓	✓		✓	✓	✓	✓	✓	I	M	

* P = Piscivore; I = Invertivore; O = Omnivore; Z = Zooplanktivore.

** R = Rare; M = Moderate; A = Abundant.

Table 7. Core fish communities of Lake Winnipeg.

Abundant Lakewide Nearshore Species	Abundant Lakewide Offshore Species	Abundant Lakewide Riverine Species
Cyprinus carpio	*Coregonus artedi*	*Coregonus clupeaformis*
Notropis atherinoides	*Coregonus clupeaformis*	*Cyprinus carpio*
Notropis hudsonius	*Notropis atherinoides*	*Notropis atherinoides*
Pimephalas promelas	*Notropis hudsonius*	*Notropis hudsonius*
Catostomus commersoni	*Catostomus commersoni*	*Pimephalas promelas*
Moxostoma macrolepidotum	*Percopsis omiscomaycus*	*Catostomus commersoni*
Percopsis omiscomaycus	*Lota lota*	*Moxostoma macrolepidotum*
Lota lota	*Morone chrysops*	*Percopsis omiscomaycus*
Culaea inconstans	*Perca flavescens*	*Lota lota*
Cottus bairdi	*Sander canadensis*	*Culaea inconstans*
Cottus cognatus	*Sander vitreus*	*Cottus bairdi*
Morone chrysops		*Cottus cognatus*
Ambloplites rupestris		*Morone chrysops*
Etheostoma nigrum		*Ambloplites rupestris*
Perca flavescens		*Etheostoma nigrum*
Percina shumardi		*Perca flavescens*
Sander canadensis		*Percina shumardi*
Sander vitreus		*Sander canadensis*
		Sander vitreus

Table 8. Trophic guilds of adult fishes of Lake Winnipeg.

Omnivore Species

Cyprinus carpio
Notemigonus crysoleucas
Notropis atherinoides
Carpiodes cyprinus
Catostomus catostomus
Catostomus commersoni
Ictiobus cyprinellus
Moxostoma anisurum
Moxostoma erythrurum
Moxostoma macrolepidotum
Ameiurus nebulosus

Invertivore Species

Acipenser fulvescens
Hiodon alosoides
Hiodon tergisus
Umbra limi
Coregonus artedi
Coregonus clupeaformis
Coregonus zenithicus
Couesius plumbeus
Macrhybopsis storeriana
Notropis heterodon
Notropis heterolepis
Notropis hudsonius
Notropis texanus

Invertivore Species cont.

Notropis volucellus
Platygobio gracilis
Rhinichthys obtusus
Rhinichthys cataractae
Moxostoma anisurum
Moxostoma erythrurum
Moxostoma macrolepidotum
Ameiurus melas
Ameiurus nebulosus
Noturus gyrinus
Percopsis omiscomaycus
Lota lota
Culaea inconstans
Pungitius pungitius
Cottus bairdi
Cottus cognatus
Cottus ricei
Morone chrysops
Ambloplites rupestris
Pomoxis nigromaculatus
Etheostoma exile
Etheostoma nigrum
Perca flavescens
Percina caprodes
Percina maculata
Percina shumardi
Aplodinotus grunniens

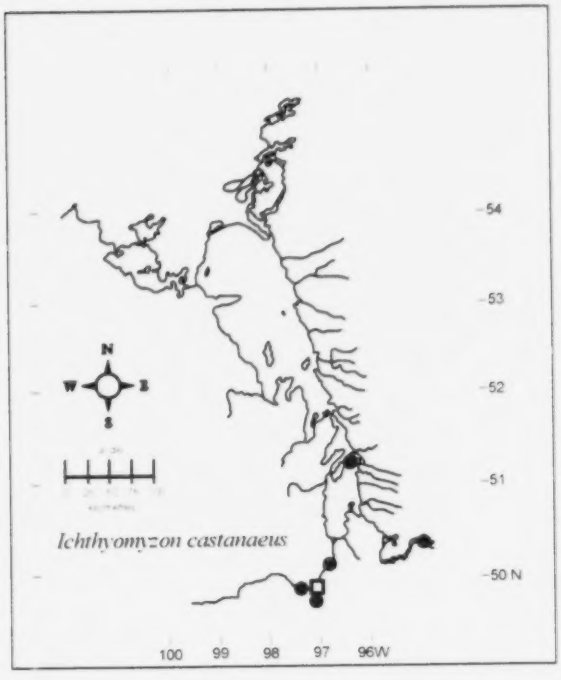
Piscivore Species

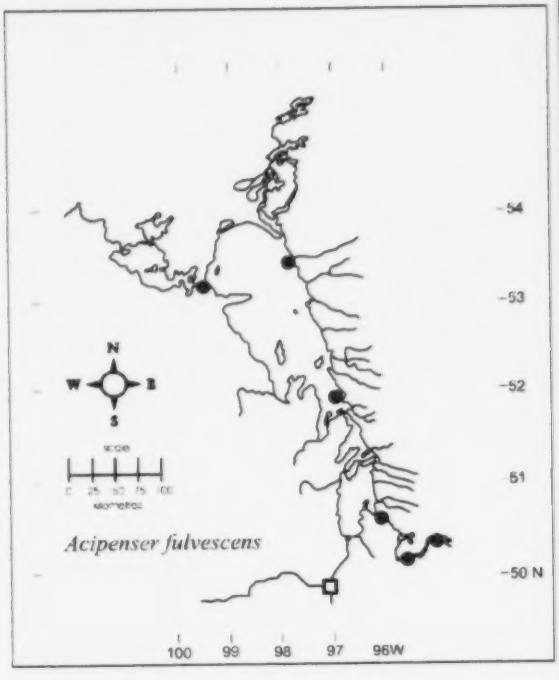
Ichthyomyzon castanaeus
Hiodon alosoides
Hiodon tergisus
Esox lucius
Osmerus mordax
Salvelinus namaycush
Ameiurus melas
Ictalurus punctatus
Lota lota
Morone chrysops
Ambloplites rupestris
Micropterus dolomieui
Pomoxis nigromaculatus
Perca flavescens
Sander canadensis
Sander vitreus

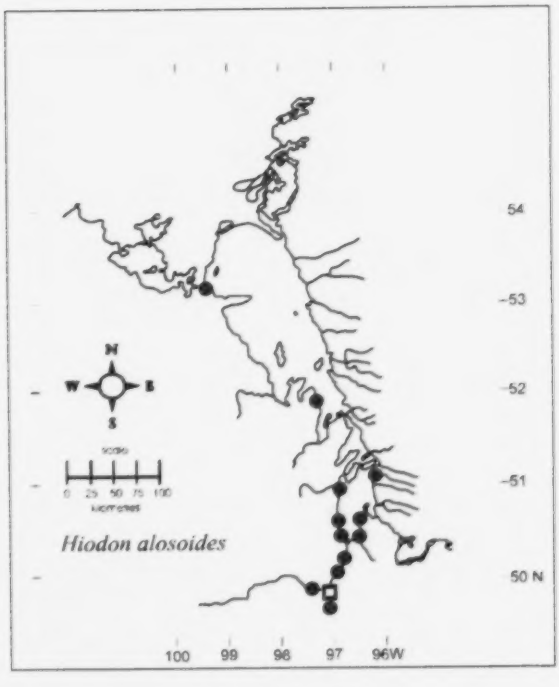
Zooplanktivore Species

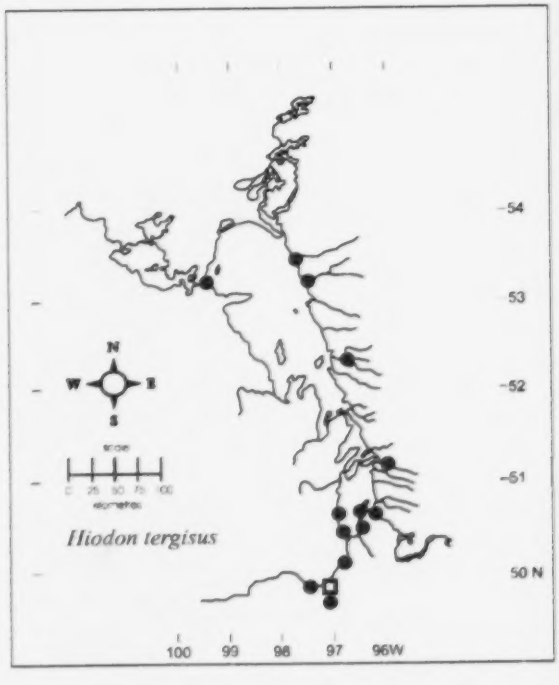
Hiodon alosoides
Hiodon tergisus
Osmerus mordax
Coregonus artedi
Notemigonus crysoleucas
Notropis atherinoides
Pimephalas promelas
Ictiobus cyprinellus

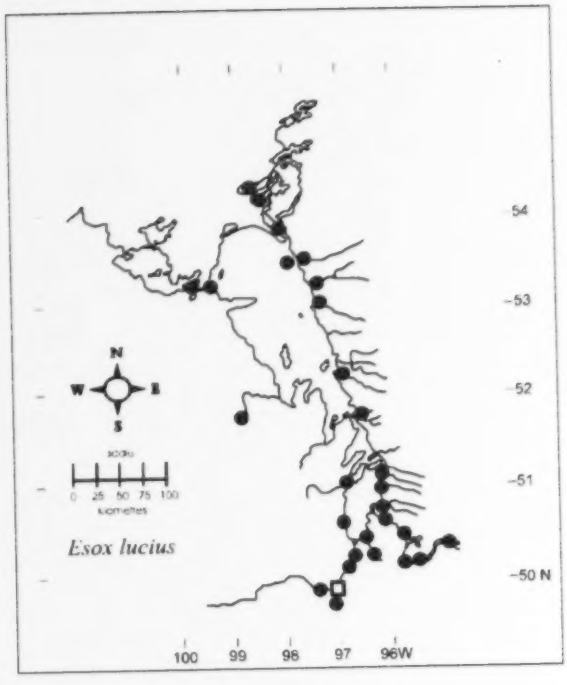
Appendix 1. Distribution records for fish species in Lake Winnipeg and its immediate basin.







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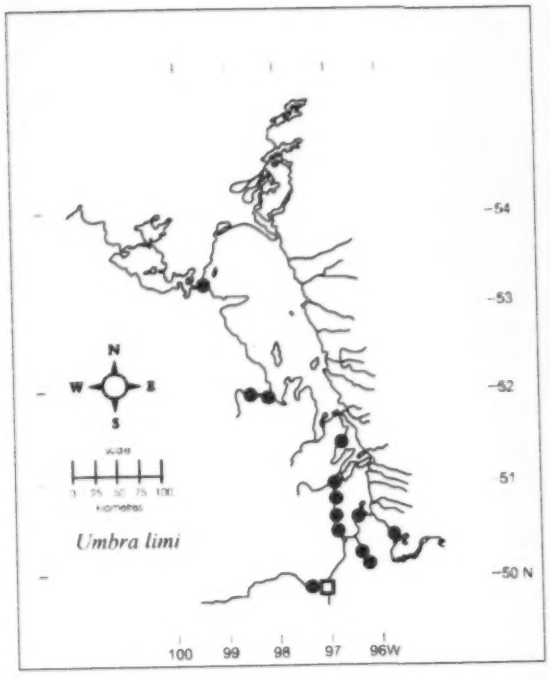
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Umbra limi
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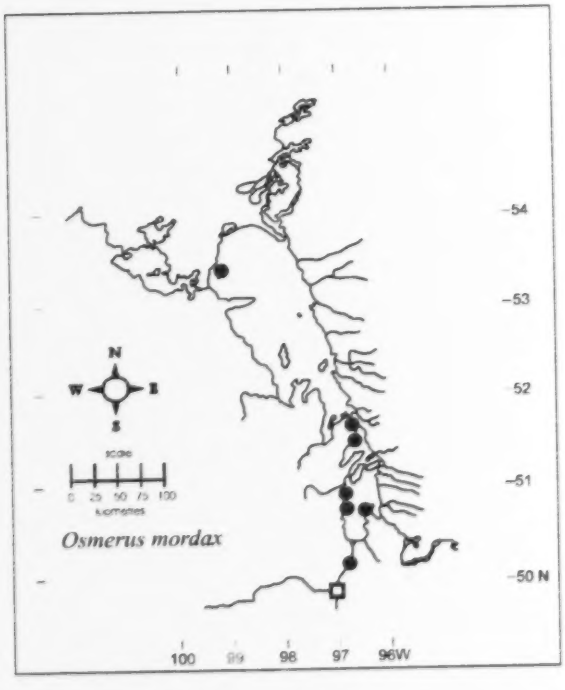
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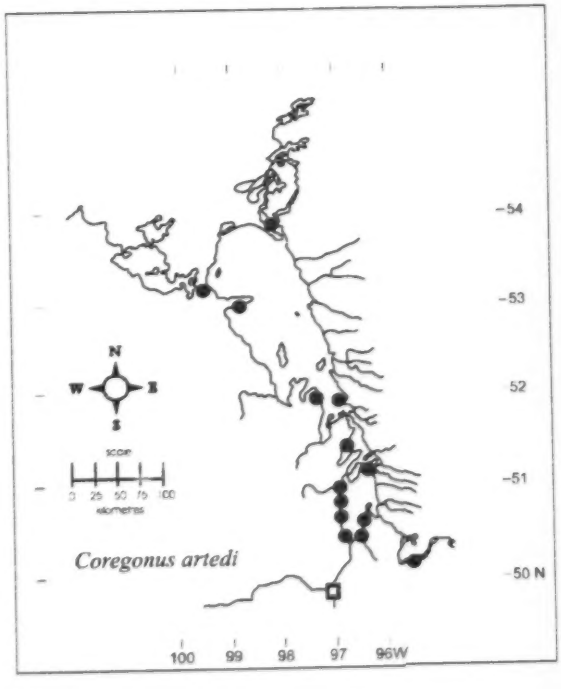
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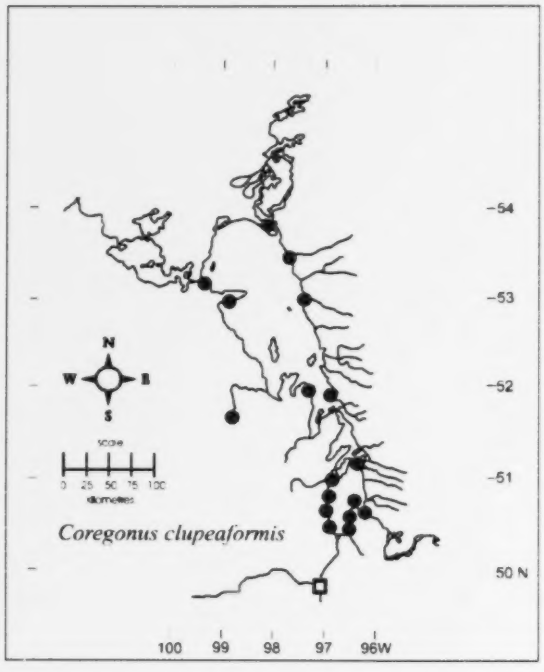
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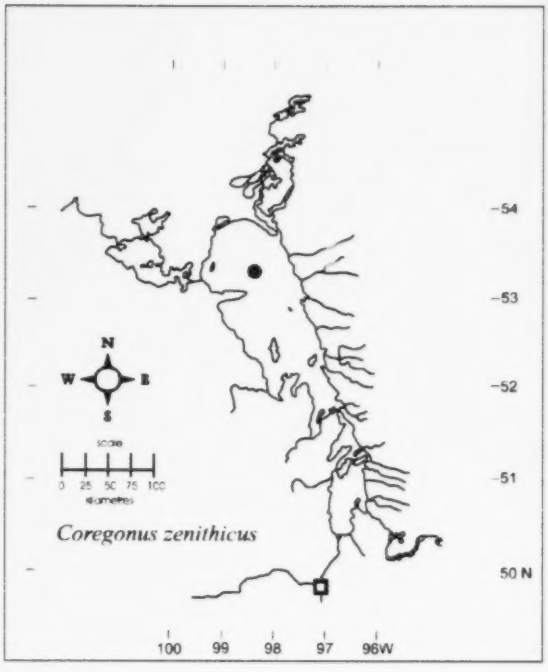
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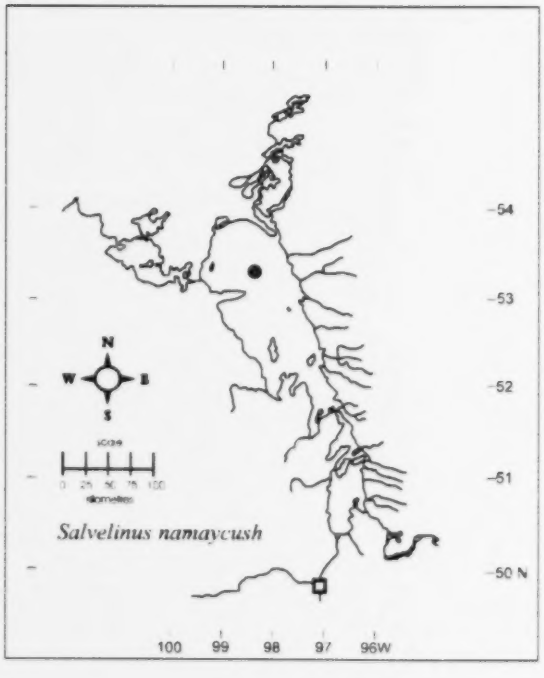
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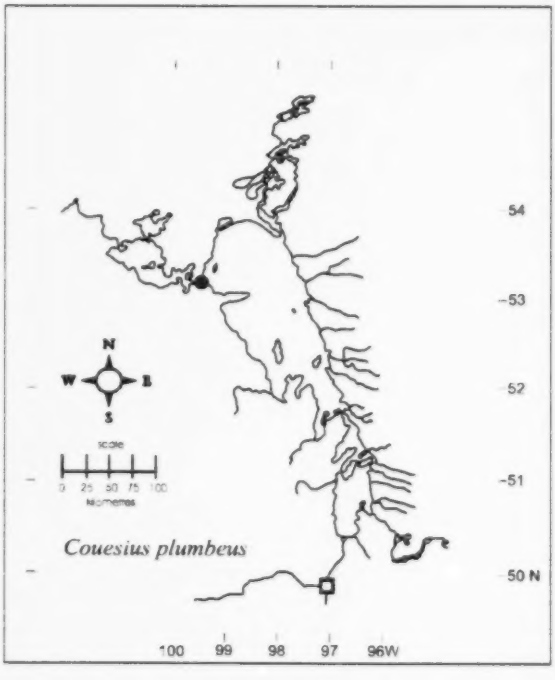
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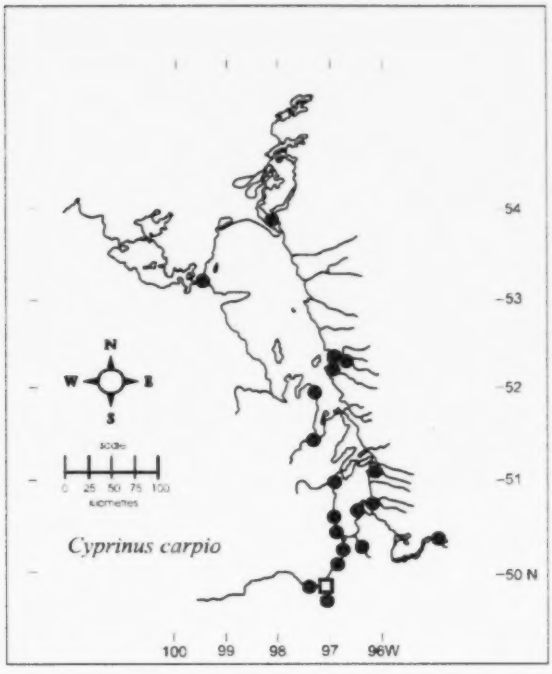
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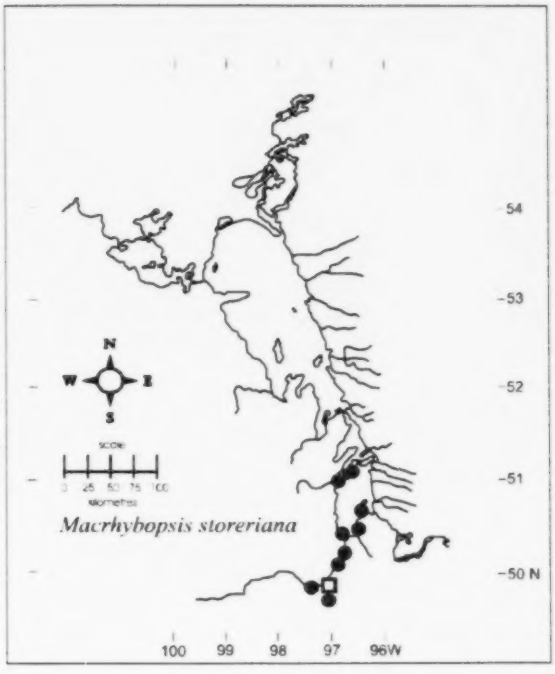
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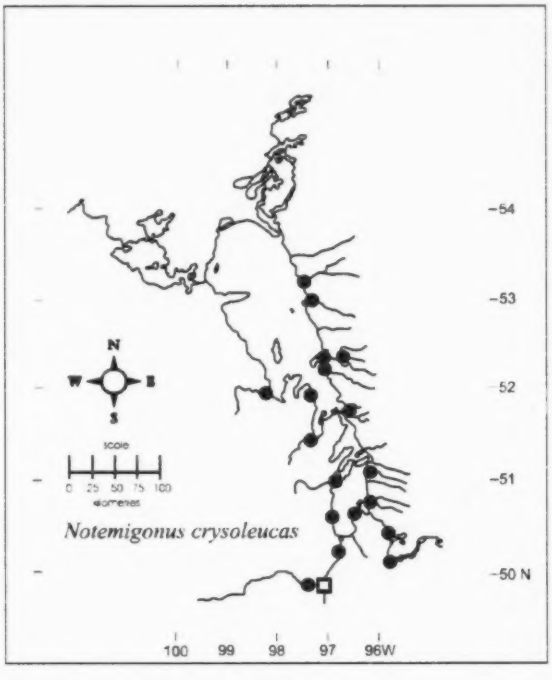
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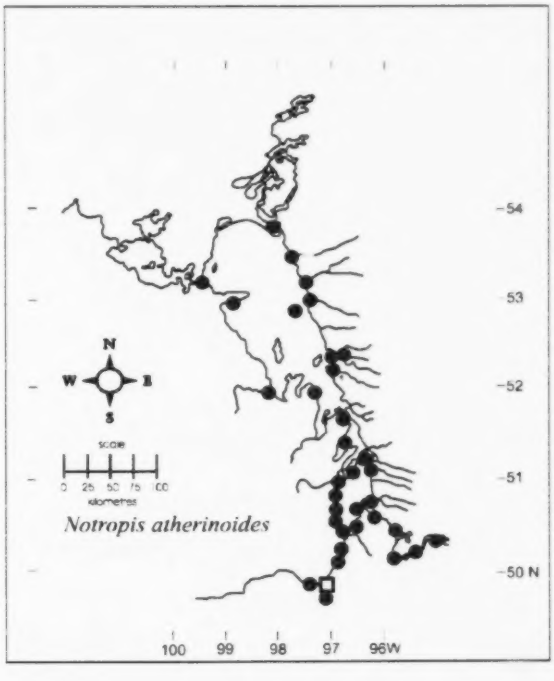
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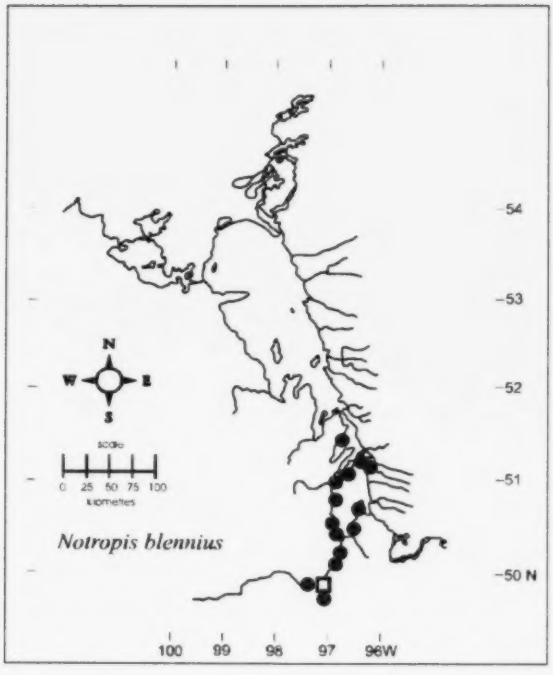
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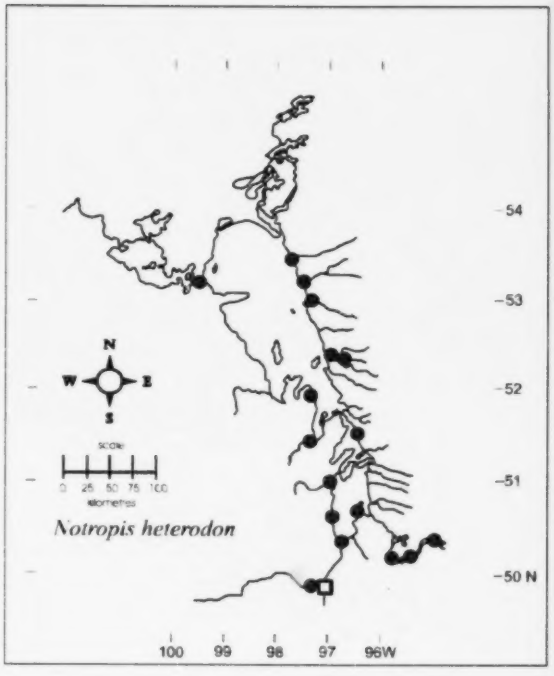
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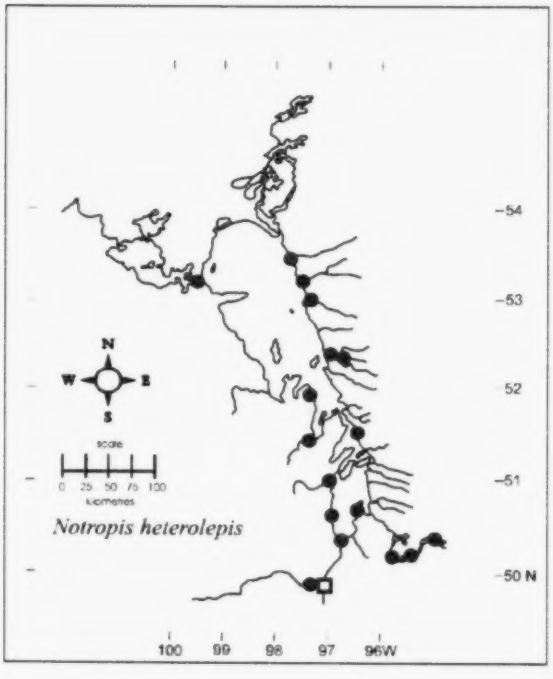
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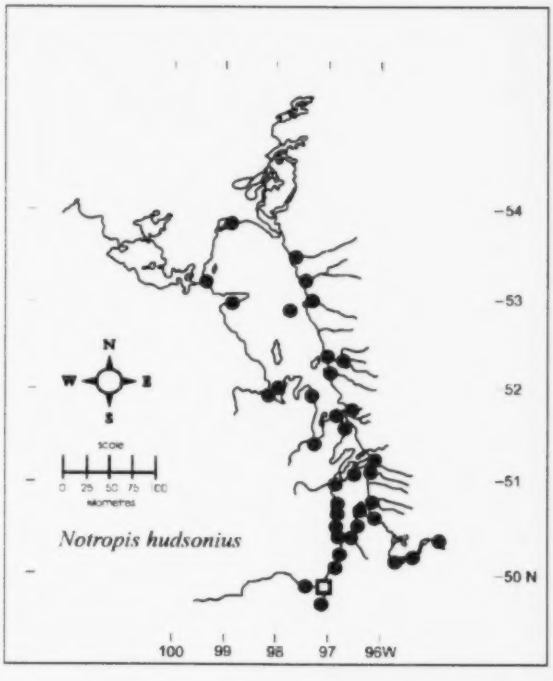
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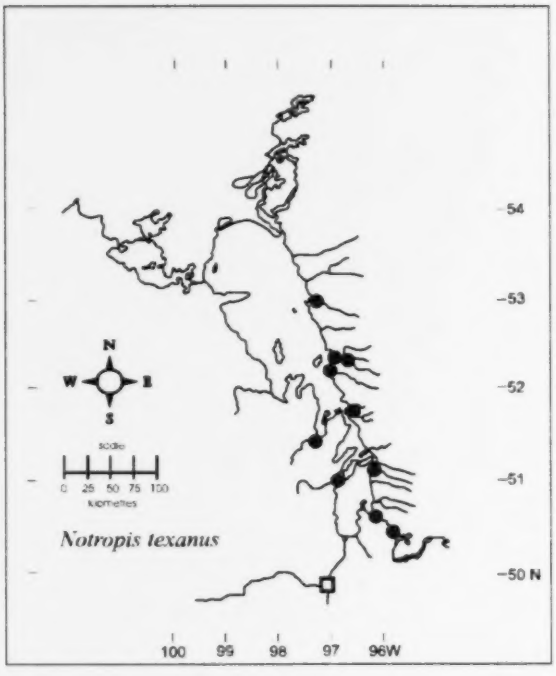
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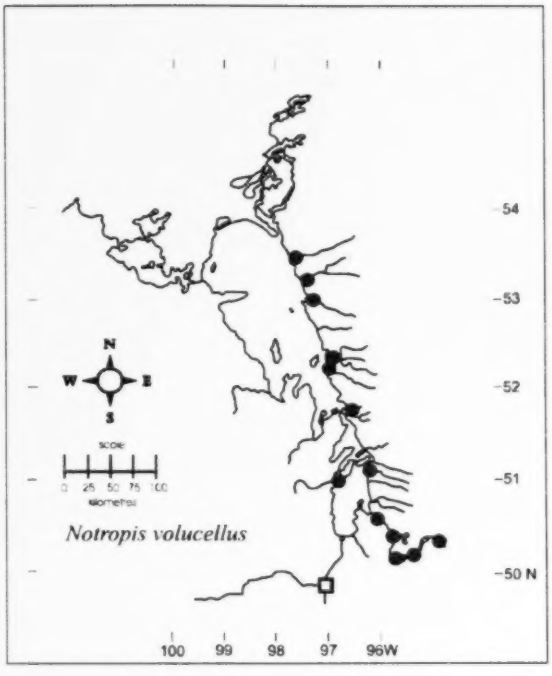
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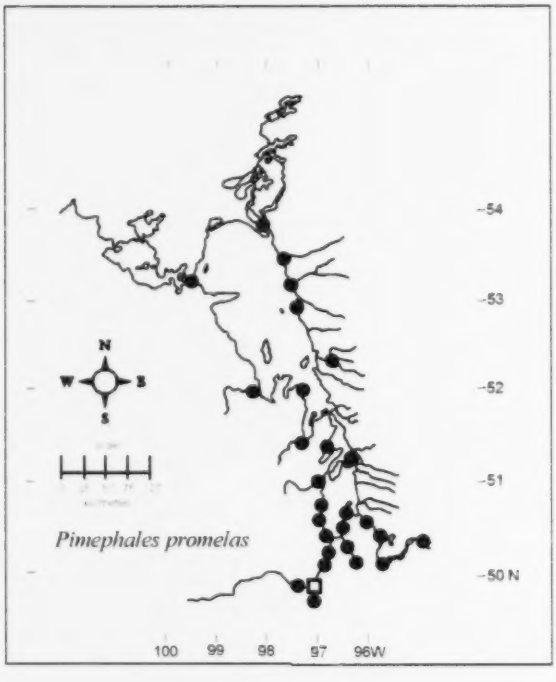
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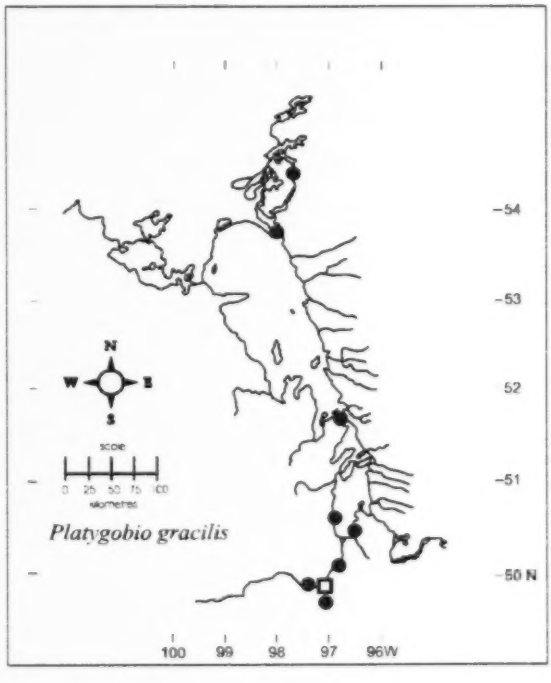
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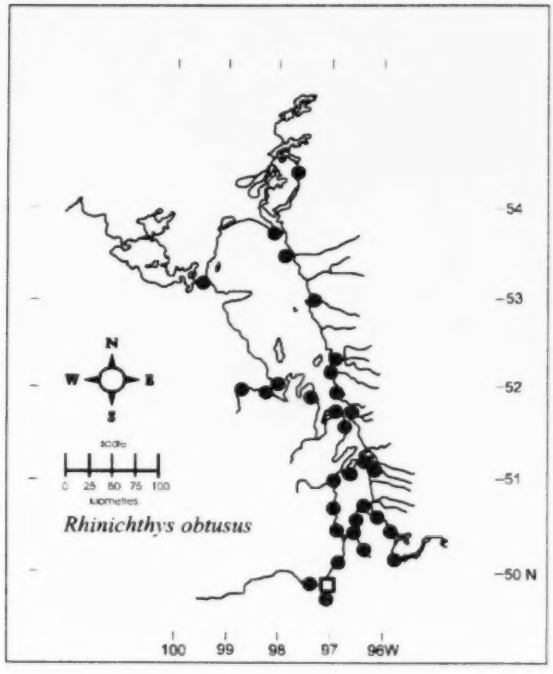
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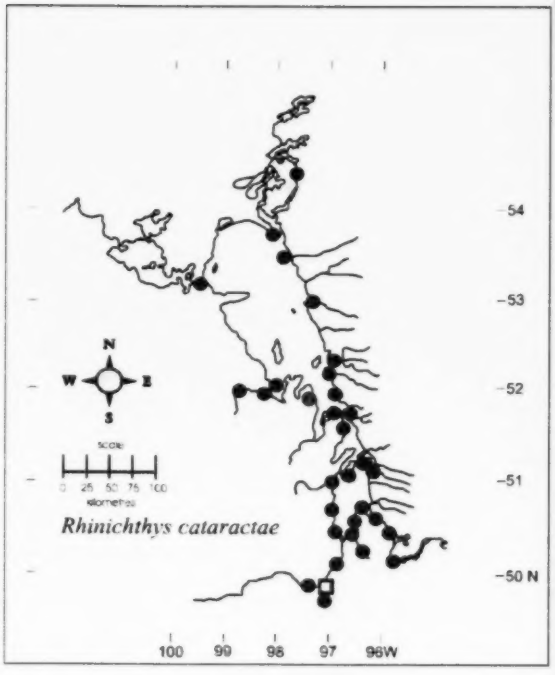
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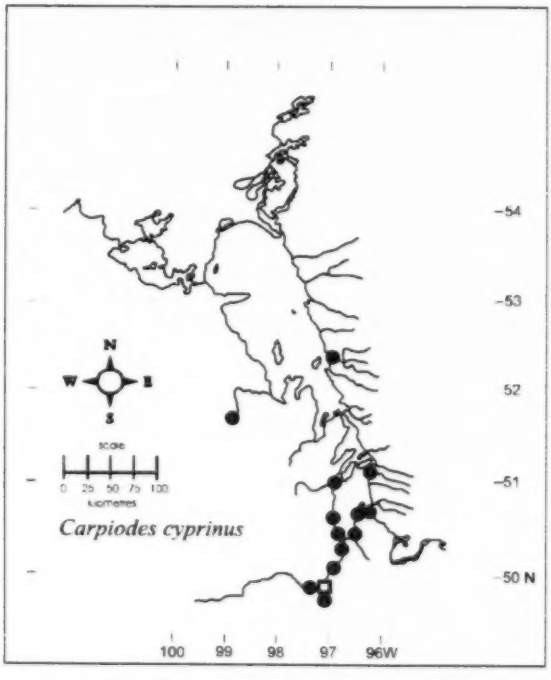
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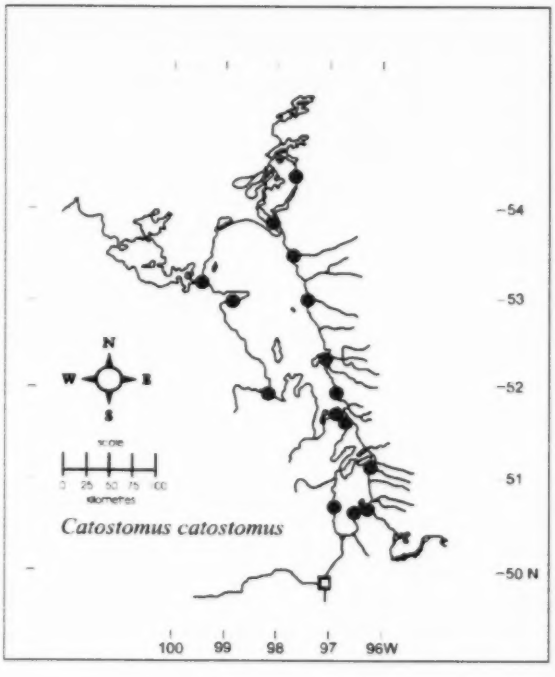
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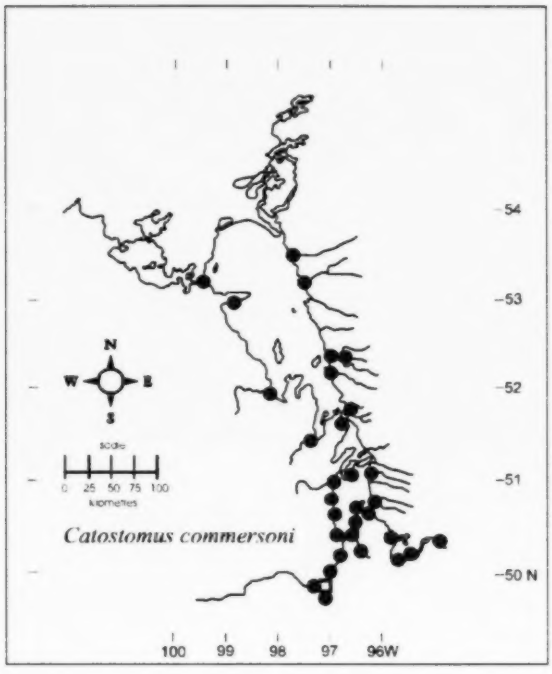
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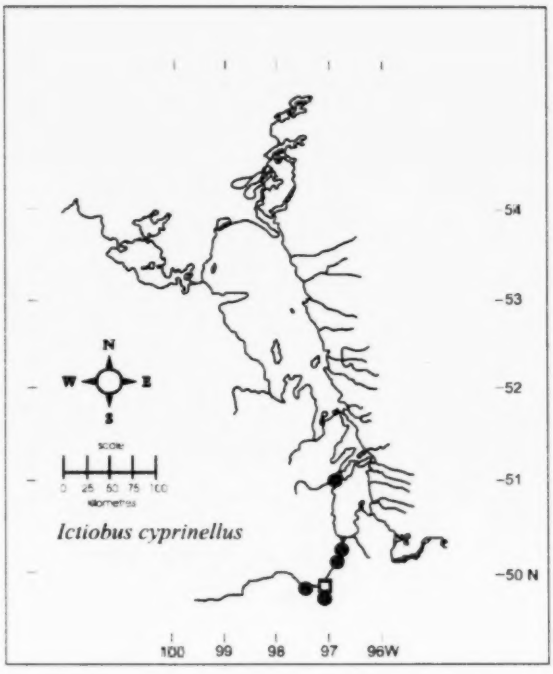
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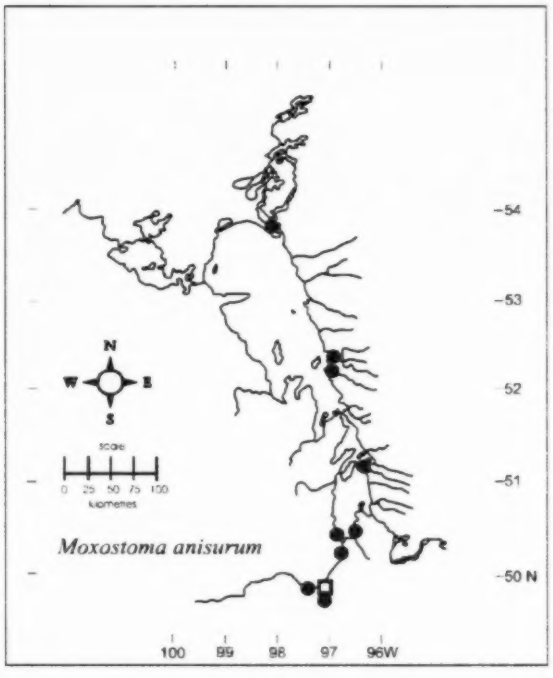
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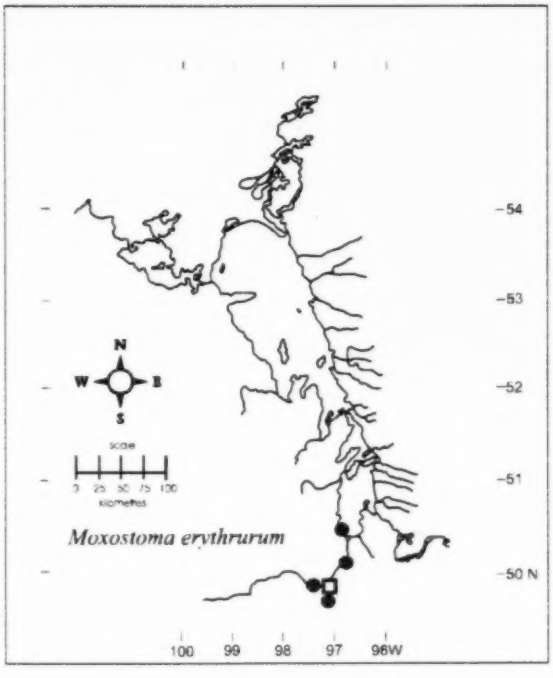
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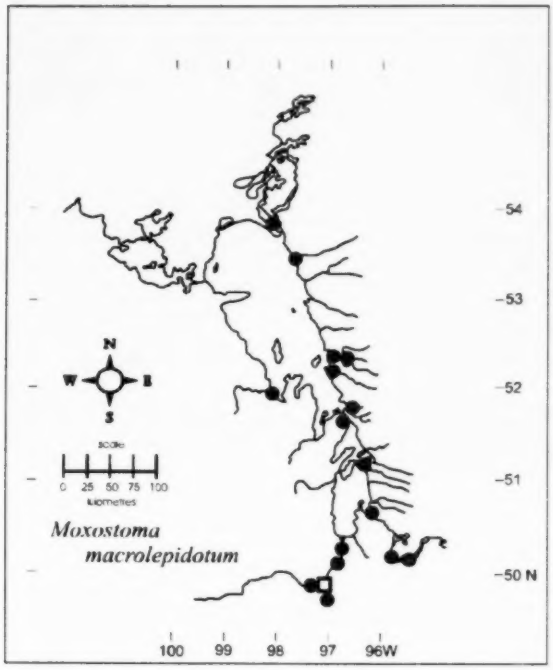
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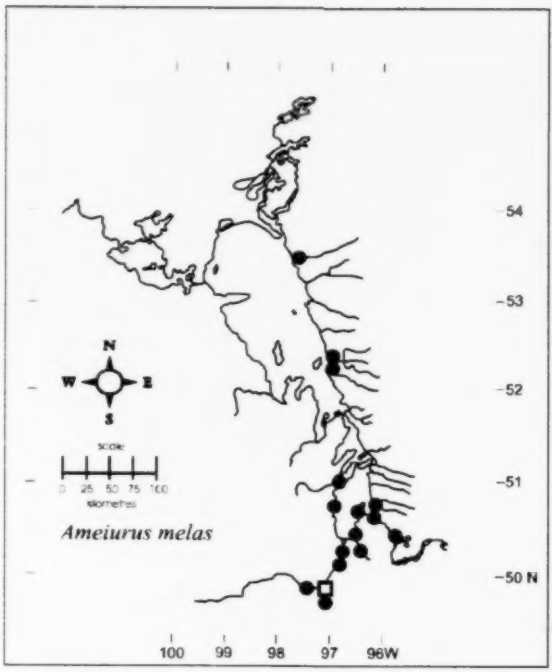
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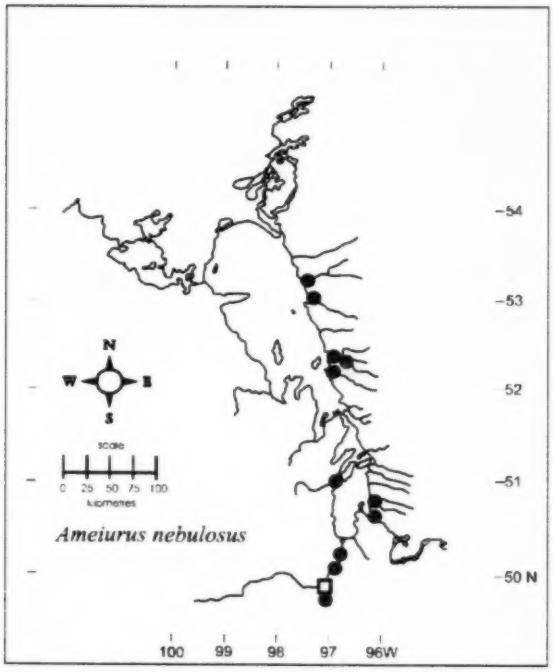
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kilometres
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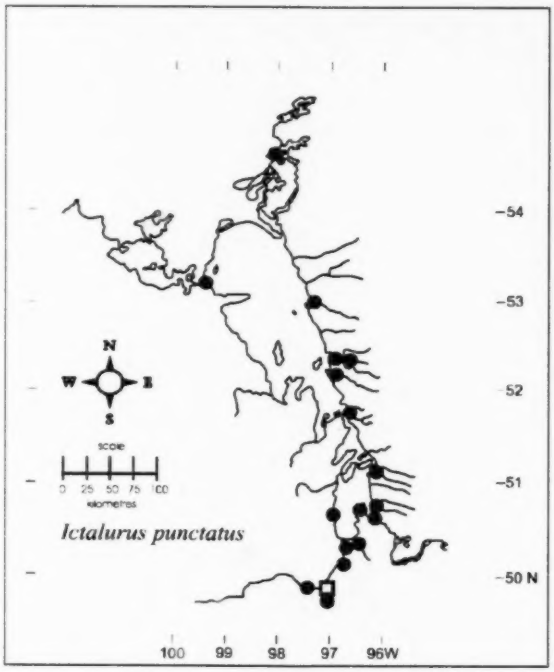
96W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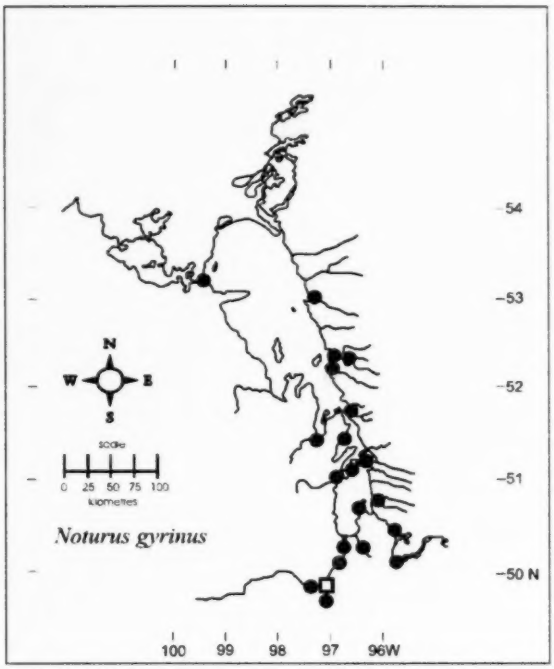
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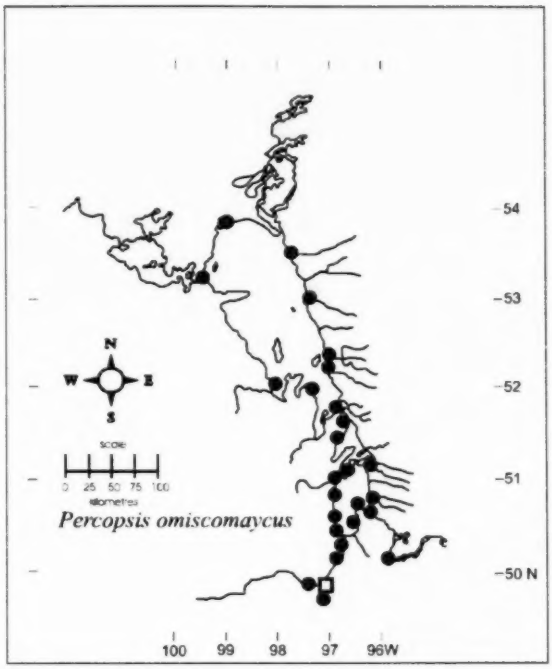
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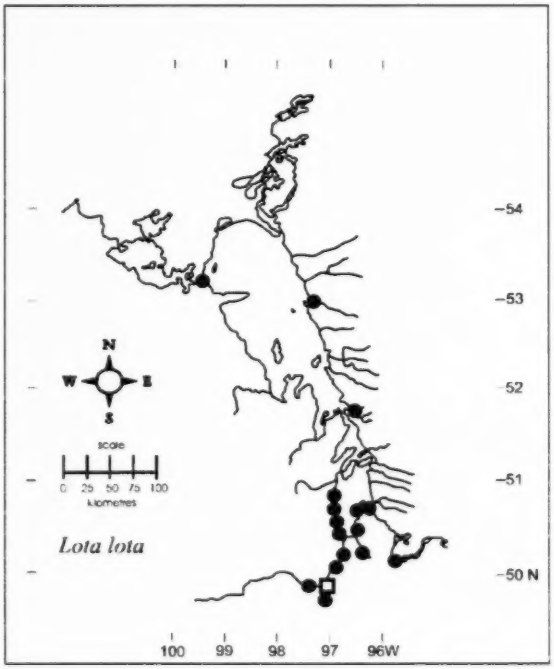
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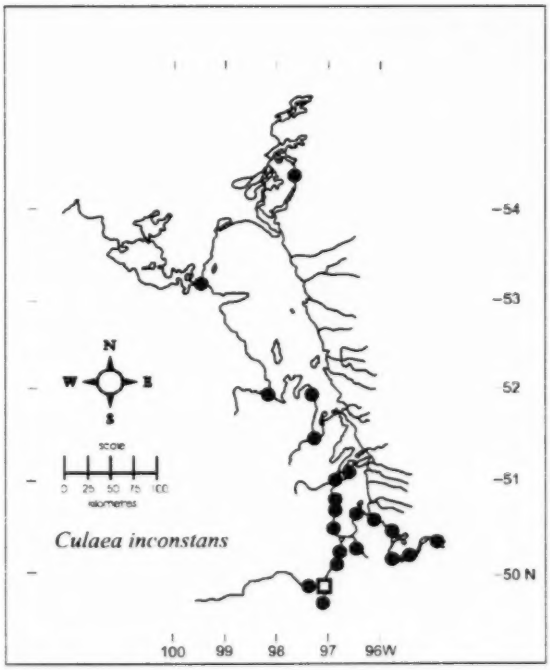
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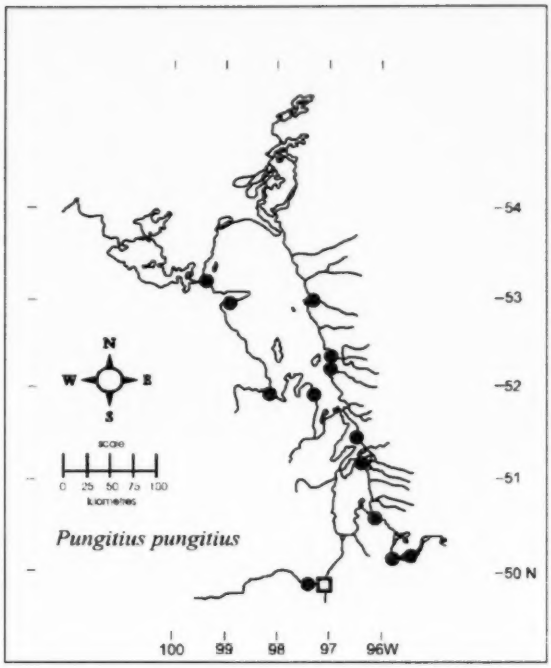
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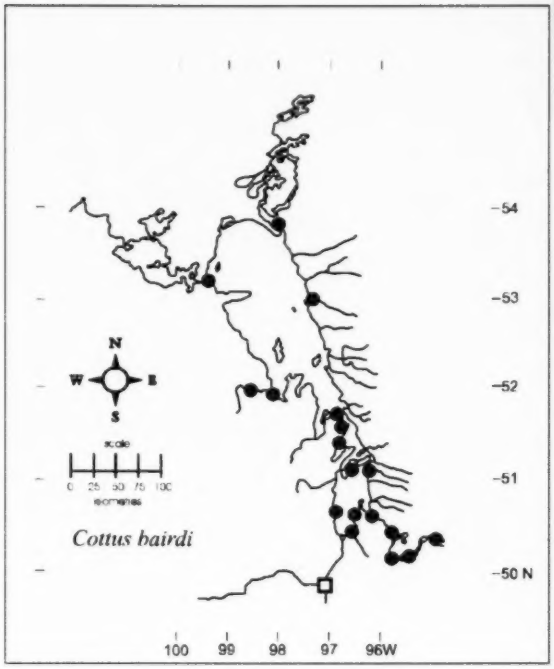
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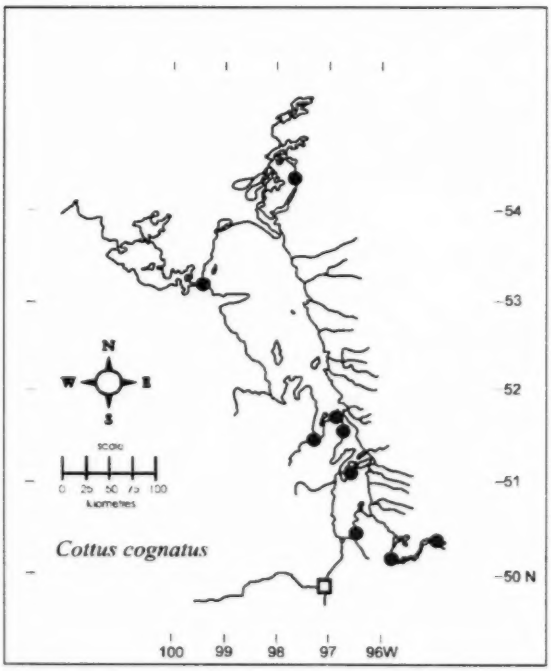
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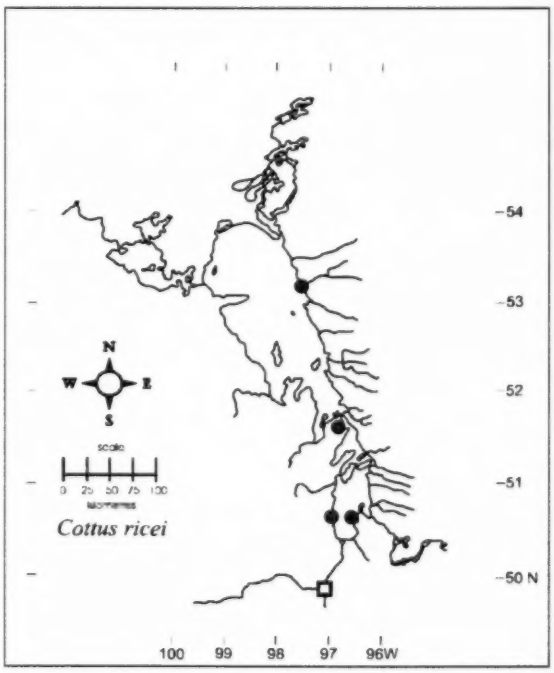
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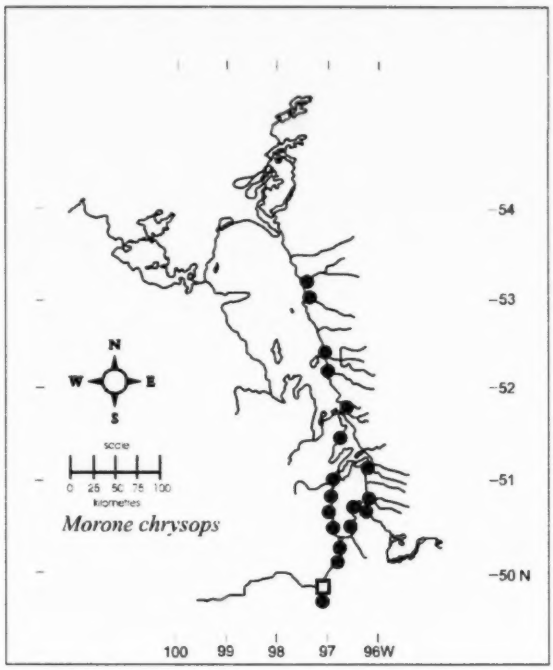
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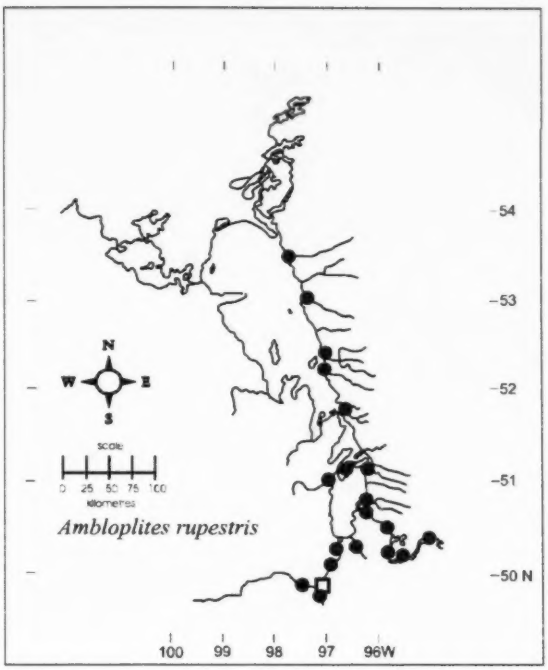
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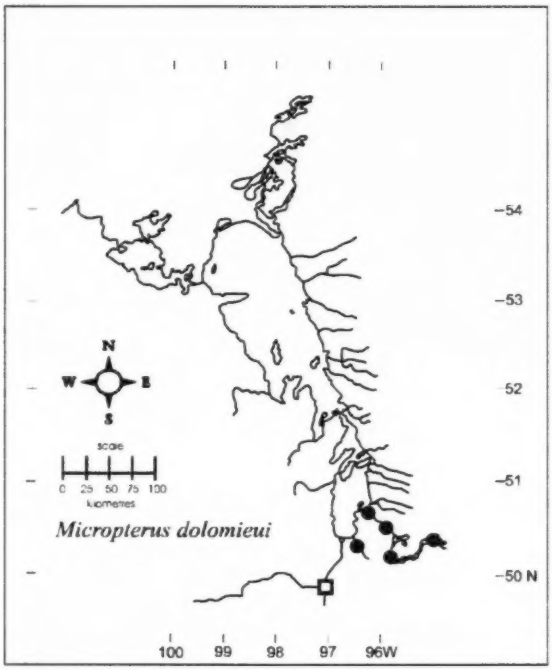
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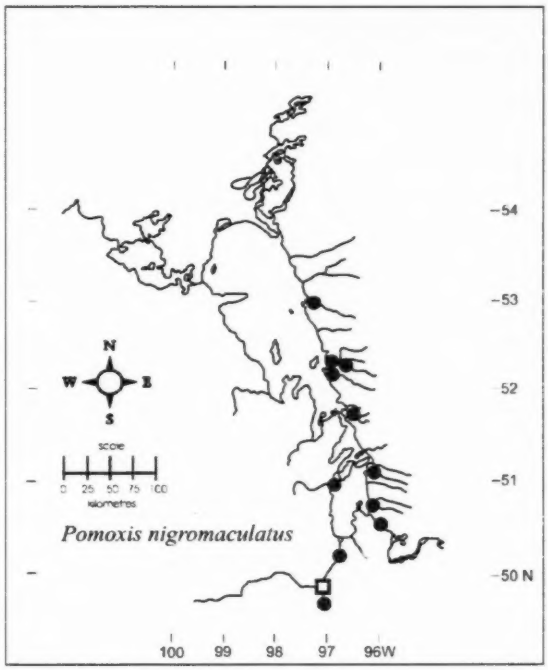
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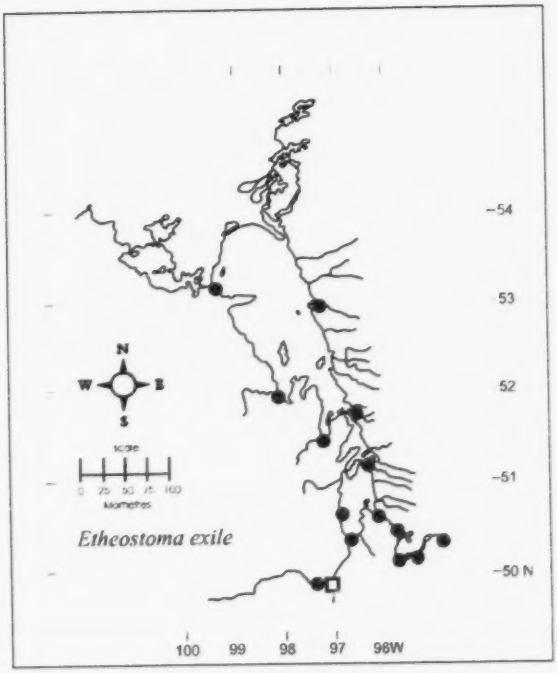
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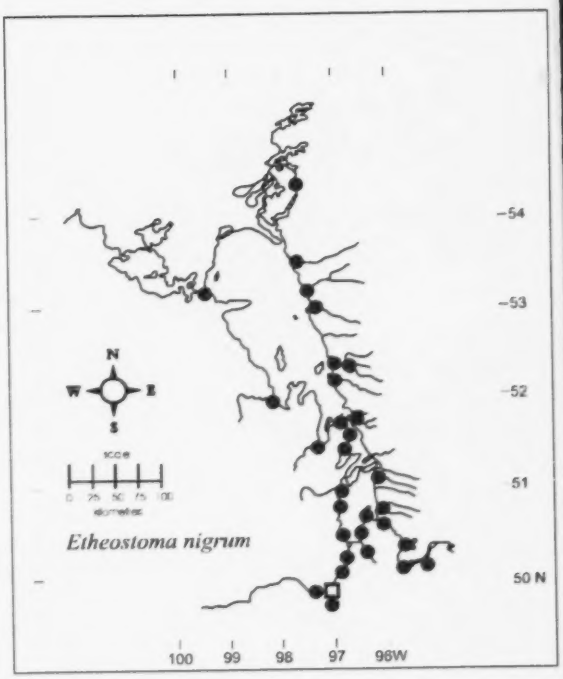
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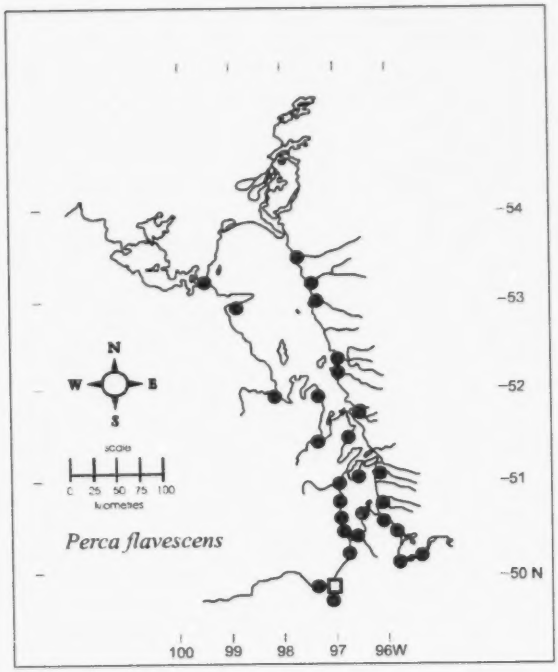
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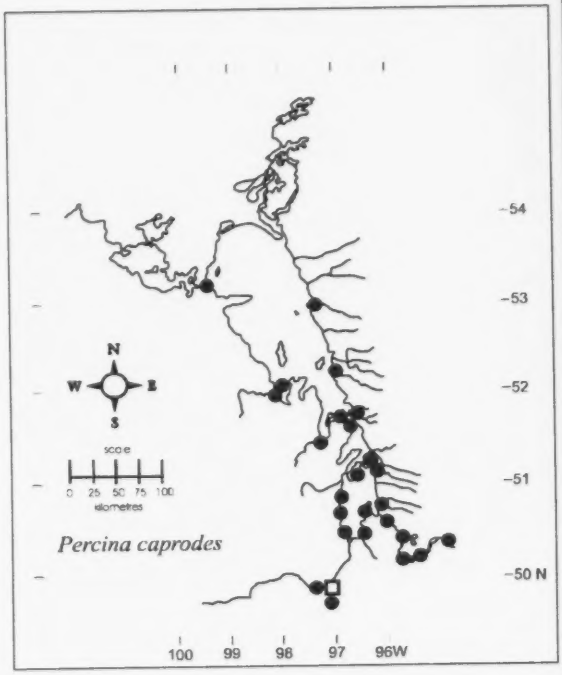
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scale
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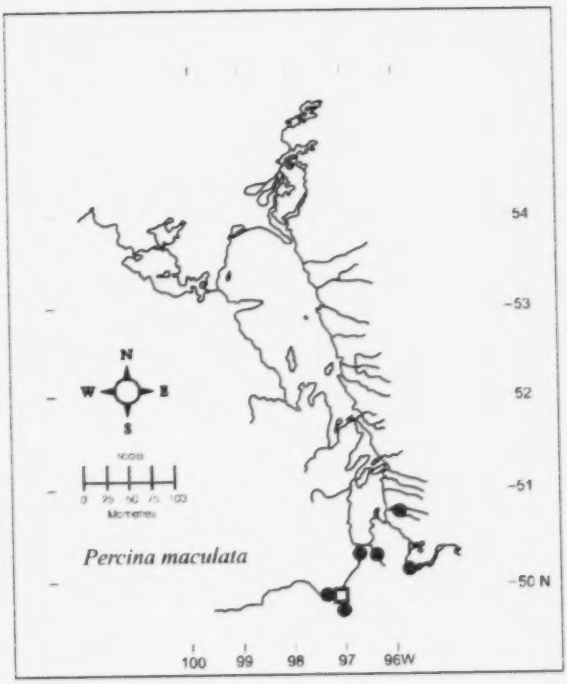
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scale
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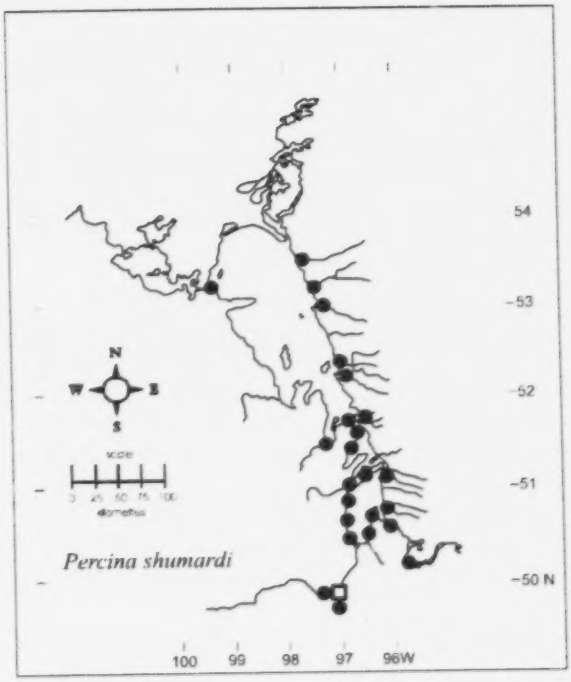
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Percina shumardi
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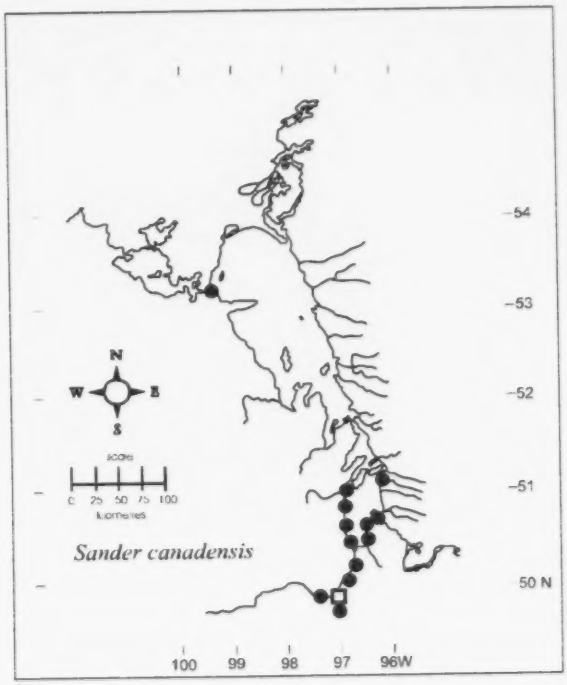
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kilometres
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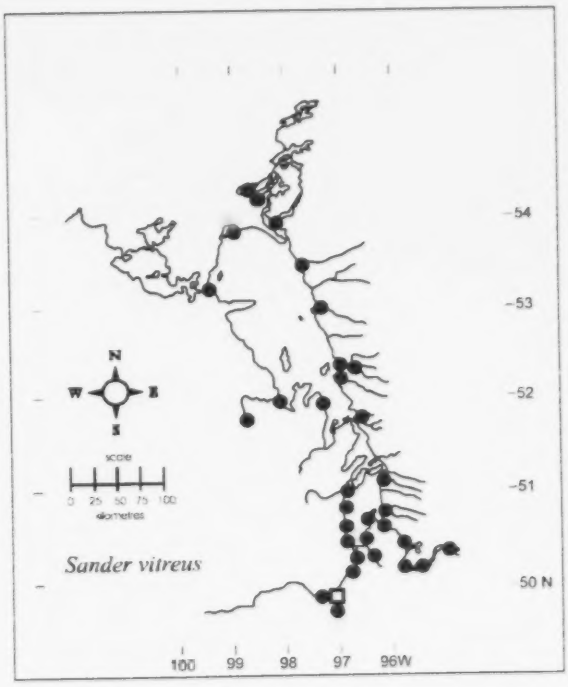
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scale
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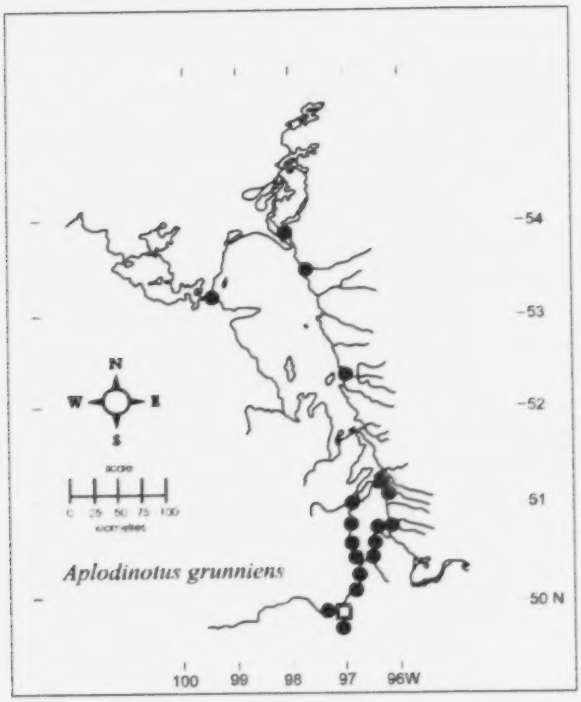
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scale
0 25 50 75 100
kilometres
Aplodinotus grunniens
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Appendix 2. Commercially marketed fish catches in kilograms from Lake Winnipeg: 1883 to 1990.

Year	Fish Species											
	Lake Whitefish	Walleye	Sauger	Northern Pike	Cisco	Yellow Perch	Lake Sturgeon	Channel Catfish	Goldeye	Mixed-Home[†]	Others[‡]	Total(kg)
1883-84	72867	-*	-	-	-	-	-	-	-	-	-	72867
1884-85	359000	-	-	-	-	-	-	-	-	-	-	359000
1885-86	759730	6455	-	-	4182	227	19091	1136	-	-	-	759730
1886-87	800000	-	-	-	-	-	-	-	-	-	-	800000
1887-88	781625	30909	-	24091	18182	-	11364	11364	-	392726	-	1270261
1888-89	1004556	99252	-	64822	47775	453	7027	1639	-	548636	5500	1779660
1889-90	1270350	127911	-	170623	27190	1637	58576	355	227	158522	55	1815446
1890-91	1546465	229867	-	338219	81227	-	85377	-	-	827562	-	3108717
1891-92	1312052	184218	-	71181	77773	-	22282	-	-	869832	-	2537338
1892-93	1712090	187640	-	37027	68182	-	42314	-	-	694990	-	2742243
1893-94	1732252	182494	-	47682	3182	-	16909	4614	-	480784	-	2467917
1894-95	1288956	454509	-	153755	153647	8379	34668	27154	-	884671	-	3005739
1895-96	1666609	364245	-	127907	122091	10659	47382	36238	-	853953	-	3229084
1896-97	1668555	398786	-	108035	104545	18545	79885	80909	-	1021275	-	3480535
1897-98	1250256	486795	-	124685	116414	21562	102554	42120	-	385726	-	2530112
1898-99	1153191	429737	-	159535	100645	29905	203414	74710	-	440013	-	2591150
1899-00	907509	292617	-	122390	65885	27733	202176	56660	11764	133909	-	1820643
1900-01	1770500	569727	-	138318	53136	21818	446136	83818	1636	173727	-	3258816
1901-02	2272727	1136364	-	454545	227273	12955	272727	250000	90909	1705045	-	6422545
1902-03	2727273	1363636	-	454545	272727	18182	272727	272727	136364	2499999	-	8018180
1903-04	3181818	1818182	-	545455	545455	454545	272727	227273	136364	2545454	-	9727273

Appendix 2. Continued…

1904-05	3409091	1931818	-	556818	818182	56818	272727	250000	136364	2727272	-	10159090
1905-06	2954545	2045455	-	568182	818182	56818	272727	227273	136364	2727272	-	9806818
1906-07	2272727	2045455	-	454545	727273	34091	90909	90909	136364	2272727	-	8125000
1907-08	909091	1250000	-	342727	568182	34091	68182	79545	181818	1250000	-	4683636
1908-09	1022727	750000	-	215909	170455	16636	36136	91682	261364	431817	-	2996726
1909-10	1576409	1017500	-	354455	311000	26364	23727	39636	380636	931817	-	4661544
1910-11	1326136	1085955	-	190409	781364	23364	92727	35955	339227	2183500	-	6058637
1911-12	1419682	1664091	-	282955	324045	27000	-	-	-	1998955	-	5716728
1912-13	1453409	697955	-	200136	382273	15864	-	-	-	1143636	727	3894000
1913-14	973455	763045	-	123630	614091	11045	-	29455	223636	467727	-	3206090
1914-15	1021636	1094818	-	197409	1588136	16136	-	34136	323091	1440909	1636	5717907
1915-16	1202409	470682	-	118318	2064136	18500	-	63000	165500	1500000	364	5602909
1916-17	1262545	656727	-	167727	1876409	368500	52636	49318	277545	1500000	-	6211407
1917-18	1279591	845500	-	182682	2033727	368318	38773	18182	344045	1500000	-	6610818
1918-19	1387500	725500	-	150136	2504409	22318	6136	31682	160091	1909091	-	6896863
1919-20	1352500	741500	-	171682	1270182	18864	5636	19864	34636	3773	509091	4127728
1920-21	1319545	962182	-	230182	1226682	3045	18045	10909	129773	43636	529318	4473317
1921-22	3243000	1393045	-	198591	1722273	6273	39727	35364	95818	-	22591	6756682
1922-23	2639400	974000	-	151773	1722045	6273	11409	35364	95409	-	18500	5654173
1923-24	1626400	1357545	-	281545	655273	82727	23955	35955	515091	-	8136	4586627
1924-25	1591000	1182455	-	292545	602182	67364	40273	63545	164273	1136	11318	4016091
1925-26	2559000	723500	-	190636	1266136	39864	31682	161182	186455	8045	17091	5183591
1926-27	3741700	1411500	-	331227	2429136	74864	14045	28682	245091	6318	51364	8333927
1927-28	2826000	1982318	100955	281818	3254773	17273	15364	65182	327773	9864	12773	8894093

Appendix 2. Continued...

1928-29	3089300	2235409	165136	297773	3270227	26364	-	46273	201409	750909	27364	10110164
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1930-31	1565727	1242227	394636	470636	1589364	25182	-	15409	162182	1045	5273	5471681
1931-32	1638318	1041727	701046	143773	165818	17773	-	7864	59364	-	16045	3791728
1932-33	2108182	1056591	867909	84364	433909	25091	-	14636	84909	-	3773	4679364
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1934-35	1889318	1760591	1881955	126409	541636	33409	-	8818	40636	1409	15864	6300045
1935-36	1361818	1371545	1326000	175955	357500	20136	-	20955	36136	2591	44454	4717090
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1939-40	922364	1469591	3929409	163182	490636	69636	4500	6909	36773	-	9819	7102819
1940-41	1591591	1791364	4043000	1394545	843364	248864	5500	3091	15909	-	14864	9952092
1941-42	1823636	1639136	4651227	137955	753864	119682	5545	5545	17091	-	10683	9164364
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Appendix 2. Continued...

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1956-57	749955	1777227	1458091	357318	1178182	177364	-	3909	9227	-	577773	6289046
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1973-74	750173	841028	1364108	281855	131014	41312	91	-	-	-	105049	3514630
1974-75	742080	833504	1163969	269677	281504	58465	-	-	91	-	216801	3566091
1975-76	829750	1017114	1227594	350806	213105	42447	25	-	239	-	113072	3794152

Appendix 2. Continued...

1976-77	779137	1212954	1130207	372502	10175	32107	-	1189	7571	-	16193	3562035
1977-78	1059474	1404754	1231479	311149	4545	30936	-	1367	1262	-	44238	4089204
1978-79	1463241	1163119	1192975	270021	1490	48853	35	3546	156	-	67426	4210862
1979-80	1586746	1237101	1154783	291304	32060	47031	56	6873	58	-	265523	4621535
1980-81	1610992	1126055	1730977	249836	78	76785	-	10257	1256	-	230976	5038962
1981-82	1477675	1758477	1528445	283073	17	81762	-	10899	1468	-	188637	5330798
1982-83	1429472	1863095	1226784	251203	203	38665	-	2283	322	-	143519	4955562
1983-84	1448083	1408331	2010848	161853	31	62050	-	783	372	-	57973	5154404
1984-85	1487748	1849899	1920677	156331	22	80067	49	2375	196	-	98199	5600288
1985-86	1258373	2242177	1407421	158631	858	34682	16	2975	82	-	99592	5223413
1986-87	1706361	1940472	1133070	135036	2158	54999	-	1691	1702	-	129403	5134599
1987-88	1542241	1366827	2300941	125005	78	110806	-	2553	1195	-	68627	5529701
1988-89	1397182	1860728	2167924	145296	2	121919	45	1106	3136	-	68848	5772071
1989-90	1105128	2220255	2037457	107727	10	134364	-	-	7914	-	21627	5653948

† Mixed-Home includes unidentified catches and locally marketed fish.

‡Others includes: in the 1880s; freshwater drum, all suckers and lake trout; in the 1890s and 1900s: none recorded;in the 1910s: freshwater drum and all suckers; in the 1920s: freshwater drum and all suckers; in the 1930s and 1940s: freshwater drum, all suckers, all bullheads, carp and lake trout; in the 1950s and 1960s: freshwater drum, all suckers, all bullheads, carp and burbot; in the 1970s: freshwater drum, all suckers, all bullheads, carp, burbot and lake trout; and in the 1980s: all suckers, all bullheads, carp, black crappies, burbot and white bass.

* (-) indicates either 0 catch or no data.